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Water Use Efficiency in Plant Growth and Ambient Carbon Dioxide Level

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ABSTRACT

This report examines the validity and explores the practical implications of the proposition that CO_2 enrichment of the leaf environment enhances plant growth and, simultaneously, decreases plant water use.

A theoretical analysis of the water and carbon dioxide balance of plant leaves was made in the form of a computer program based upon known physiological facts. It predicts significant increases in water use efficiency by plants as CO_2 is enriched, the size of the increase depending upon the external conditions.

Experimental tests were conducted in an environmental simulator with stands of soybean, pepper and southern pea plants. The predictions of the model were substantially verified, with CO_2 concentrations ranging from normal to six-fold normal.

Although CO_2 is obviously an ideal antitranspirant, the efficacy of its release in open stands is doubtful in view of plausible economic factors. But, in enclosures this would be a different matter, and for such situations the present report gives a scientific basis for engineering and system analysis.

1. INTRODUCTION

A number of proposals have been made and tested with the objective of reducing the amounts of water lost by plant transpiration. Among such have been the coating of leaves with a substance that would make it less permeable for water, or with a substance that would increase its reflectance for shortwave radiation. Also, it has been proposed to spray leaves with bioactive compounds that would induce stomatal closure. A similar effect can, of course, be obtained by withholding water from the root system and, thereby, partial or total stomatal closure, and a reduction in transpiration.

Without exception the above ideas, when tested, have been found to also affect carbon assimilation and crop growth as one would expect. The question then becomes one of a trade-off between reduced yield and reduced water consumption. In this research project, a method for transpiration reduction is being investigated that does have the anticipated result of increasing growth while reducing transpiration.

It has been known for sometime that increasing the carbon dioxide level will promote carbon assimilation and growth by plants and this principle is in practical use in greenhouse culture. It has also been found that CO_2 enrichment induces partial stomatal closure, though the explanation of the effect remains controversial. Thus, one expects a reduction in transpiration and an overall effect of increasing the mass flux ratio of carbon dioxide to water, which is one way of defining water use efficiency.

Although this effect has been alluded to in the literature and some isolated data support its validity, there has been no

systematic study of the effect. The purpose of this work was to provide a comprehensive theoretical and experimental basis,under conditions representative for the field,on the carbon dioxide effect. From it we hope to deduce a value judgment concerning the feasibility of carbon dioxide enrichment as a means to increase water use efficiency.

2. THEORETICAL ANALYSIS AND MODELING

It would obviously be possible to approach the problem experimentally, growing plants at different carbon dioxide levels and to note, other conditions being equal, what the response of the plants was regarding water use, growth and other pertinent aspects of performance. The weakness of this common strategy is that there are so many combinations of the "other" conditions that a rational choice is not possible. Also, it is obviously not feasible to examine every combination since a single experiment may involve 6 weeks of intensive work, not counting data analysis.

We decided therefore to attempt a theoretical model of plant behavior in which the environmental parameters would appear as variables and to examine the predicted effect of CO_2 enrichment first by computation and, subsequently, to see if the calculated relation would correspond well with the observed ones. As it was, the theoretical and the experimental efforts were more or less parallel.

In modeling plant behavior we imposed some simplifying constraints. First, we considered only the behavior in the light as it occurs in the day time. The variables then examined are net photosynthesis (NP) (which should be more appropriately called the light flux or photoflux of CO_2) and the transpiration rate (E). Furthermore, the analysis was restricted to leaf behavior, rather than whole plant behavior on the premise that both NP and E are functions of the leaf.

Because of these restrictions, the model will not be directly applicable to prediction of dry matter accumulation over time, inclusive of dark periods, and to yield predictions. Neither will it state

anything on water use other than by transpiration.

The leaf action model is based on the principles of energy balance, water balance and carbon balance and takes account of a variable stomatal aperture, leaf temperature and leaf water potential. The environmental variables, besides the ambient carbon dioxide level, are the air temperature, air humidity,incident radiation, and wind speed. Certain physiological plant variables such as stomatal resistance, resistance to water flow in the plant, leaf size and others that bear on plant water relations are also used as variable parameters.

The details of the model are documented in the Appendix 1, which is a manuscript submitted for publication. In view of the many variables and interrelations, several of which are implicit, the model is a computer program. This program is given as Appendix 3, omitting the plotting instructions that were used to obtain solutions in graphical form as shown in Appendix 1.

For a detailed review of the theoretical results we refer also to Appendix 1. The principal result of the simulation is to suggest that carbon dioxide levels must be raised appreciably - double or triple the ambient concentration of 320 ppm - to show substantial effects upon transpiration losses. However, because the effect on carbon assimilation is, by comparison, stronger,particularly at the lower CO_2 levels, the total effect on water use efficiency, the mass flux ratio, is considerable. This is illustrated in Figure 1, in which the effect of the CO_2 level is given for several values of RLMIN. This parameter is indicative of the combined effect of stomatal frequency, size and depth with the value 10 a probable lower limit as possibly found in sunflower or alfalfa, and the value 100 as probably

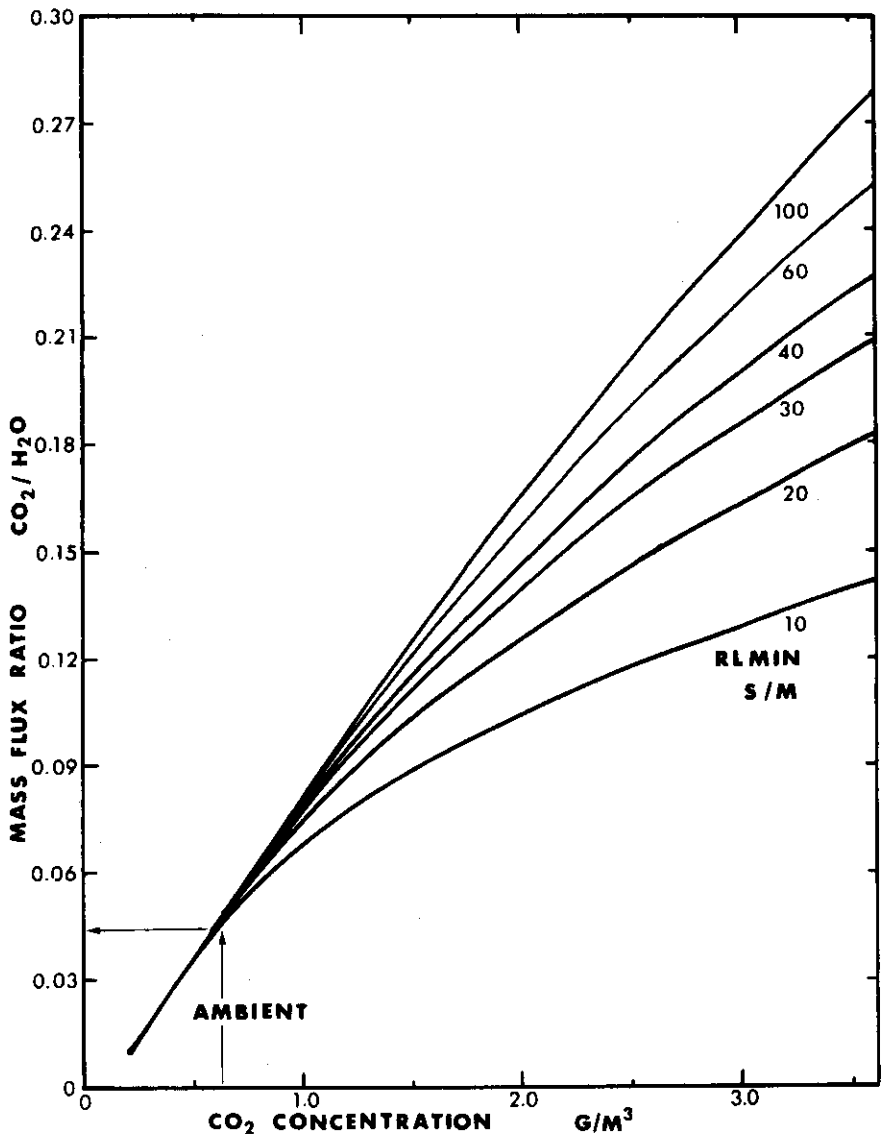

Figure 1. Effect of ambient CO_2 level in g/m^3 upon the mass flux ratio between CO_2 and H_2O for a leaf exposed to 300 W/m^2 photosynthetic radiation, 30 °C air temperature and 2 m/s windspeed. The relation is shown for several values of the lowest possible stomatal resistance in s/m.

representative of some tree species, such as citrus or oak.

A fourfold increase in the ambient CO_2 level, to about 2.3 g/m^3, results in an increase in mass flux ratio of similar proportion depending upon stomatal resistance. The expected benefit of CO_2 enrichment is greater in leaves that offer more resistance to gaseous diffusion, the more so as the CO_2 level rises.

It is to be noted that the expected mass flux ratio at ambient level, about 0.03, is higher by a factor of 2 or 3 than commonly reported maximum figures for water use efficiency in crop production. This is so because the latter figures are generally based upon harvestable dry matter, rather than total carbon dioxide equivalent, and reflect dark period losses by respiration, as well as water use other than by transpiration. The effect, then, under actual production conditions, will be less pronounced than Figure 1 suggests.

An additional important general result of the simulation is the enhancement of CO_2 effects by humidification of the air. Figure 16 of Appendix 1 shows how sensitive the basic mechanism discussed in this report is to variation in the water vapor concentration. Since the simulation of Figure 16 was done for a constant air temperature the results may also be read in terms of relative humidity, with strong effects between 70 and 90% RH. Part of the explanation is in the fact that increasing the humidity increases, by indirect action, the stomatal aperture and, thus, promotes CO_2 assimilation. In experiments in our laboratory, not related to the present work, we have found this influence demonstrated in sorghum and in southern peas.

In sum, a rather complete analysis of leaf action that involves a number of approximations and working hypotheses, affirms the notion

that CO_2 shall act as an ideal antitranspirant by simultaneously enhancing carbon assimilation and depressing water use. Further, it gives us a tool to anticipate how this action will be modified by environmental and plant characteristics.

3. EXPERIMENTAL PROCEDURES

A. Environmental simulator

Significant work on transpiration losses and carbon exchange by plants is possible only in a realistic and carefully controlled environment. A unique facility has been completed for this purpose. The nature of this test facility will be described. Reference is made to Figures 2, 3, and 4.

The plant chamber (A) is part of a closed air circuit. The chamber has a cross section of 60 x 60 cm and an overall length of 120 cm. A root compartment (B) has a depth of 15 cm. It can be open to the plant compartment or it can be closed.

The lamp compartment (F) contains ten 400-watt Lucalox lamps, operating at 208 volts from individual ballasts. The lamp compartment is separated from the plant compartment by 3 millimeter sheet of transparent plastic (Lucite). This material has shown no sign of deterioration over approximately one year's use. The heat from the lamp is carried off by a chimney and fan (G) with a displacement of approximately 10 m^3/min. Ambient air is drawn into the lamp compartment and the temperature rise is held below 10°C. The plastic barrier (I) may have temperatures up to 45°C.

Air is driven around the circuit by the fan (D), having a displacement of approximately 30 m^3/min. Thus, the air speed through the plant compartment is slightly over 1 m/sec. It cannot be varied. The air is filtered and straightened by a set of fiberglass air filters located in position (J).

The principle of control in this chamber is to cool the air continually to the desired dewpoint in the cooling coil (C), through

which chilled water runs at a rate of about 20 l/min. The water that is condensed can be measured and considered as the transpiration rate of plants in compartment (A) over periods of 30 minutes or longer.

After cooling, the air is heated by a strip heater (E) with a maximum heat input of 4 kw. It may be seen then, that the control depends on a constant rate of cooling, which is balanced with a variable rate of heating against other losses or gains of heat. The entire chamber is insulated with 5 cm rigid polyurethane foam, making the sensible heat losses quite small, a fraction of a Kw under most operating conditions. Most of the heat gained is derived from the radiation of the lamps which is estimated at approximately 1 Kw. Obviously, this type of control is wasteful of power, especially at low dewpoints. However, it is capable of great precision, approximately 0.1°C for both dewpoint and air temperature, and of rapid response, of the order of 10 to 20 seconds.

The entire system can be hermetically closed by a means of a continuous double coat of epoxy paint on the inside and rubber gasketed doors in front for access. The main construction is 20 millimeter marine plywood with 5 x 10 cm wooden beam reinforcements where necessary. The front of the lamp compartment has armholes for rubber gloves, so that plants can be manipulated and measurements made without disturbing the seal.

The control circuits, somewhat simplified, are shown in Figure 2. The lamp circuit with a total power dissipation of 4.5 Kw is controlled by an ordinary time switch (3) which allows the setting of the light and dark periods. A limit switch (2) guards against overheating of the lamp compartment. The lamp cooling circuit is operated by a

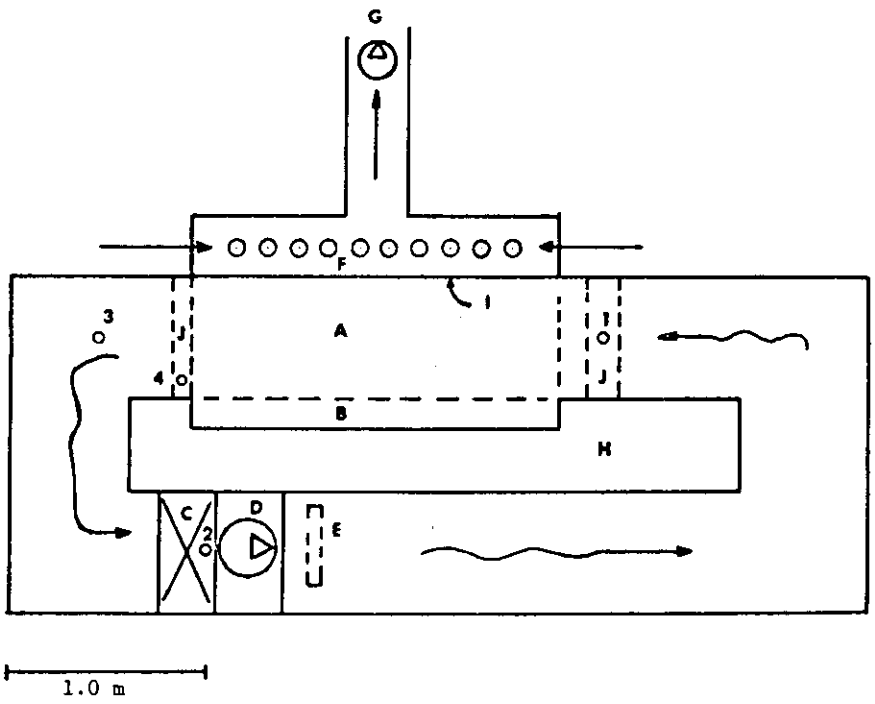

Figure 2. Environmental Simulator

A. Plant compartment
B. Root compartment
C. Cooling coil
D. Fan
E. Heater
F. Lamp compartment
G. Fan
H. Instrumentation and control
I. Lamp barrier
J. Air filters
1. Temperature measurement
   Humidity measurement
2. Temperature measurement
3. CO_2 injection
4. Steam injection

separate time clock (5) which insures that the fan (6) will start and stop well before and after the designated burning period of the lamps.

The heating rate is controlled by a thermocouple at position 1 (10). The copper-constantan wire is connected to an automatic ice-point reference device and the resulting millivoltage is led to a 0-18 millivolt controller (12, Leeds and Northrup Electromax) with an output of 0-5 ma. This control current operates a silicon controlled rectifier power regulator (8). It operates at 208 volts and can vary the power to the heating circuit (9), from 0 to approximately 4.5 Kw. The heating circuit is protected by a limit switch (7), located in close proximity of the heaters against fan or control failure. A temperature reading below the set point causes the heating current to increase and vice-versa. The response of this system is rapid, on the order of 2 or 3 seconds.

The dewpoint is controlled by regulating the temperature of the cooling coil. A thermocouple in position 2 (13) is located on the cooling coil itself and its output, after ice-point compensation, is fed to another Electromax controller (14), the control current of which is converted by an electropneumatic converter (15) to a variable air pressure. This pressure in turn, controls the opening and closing of a 3-way valve (18) which causes a greater or smaller amount of water to be taken from the chilled water supply (17) and to be circulated through the coil (20) by action of the recirculating pump (19). If the cooling coil temperature is above the set point, the control current will increase and so will the control air pressure causing the valve to open at the side of the chilled water supply and to close at the recirculating side, thus, tending to lower the temperature of the water

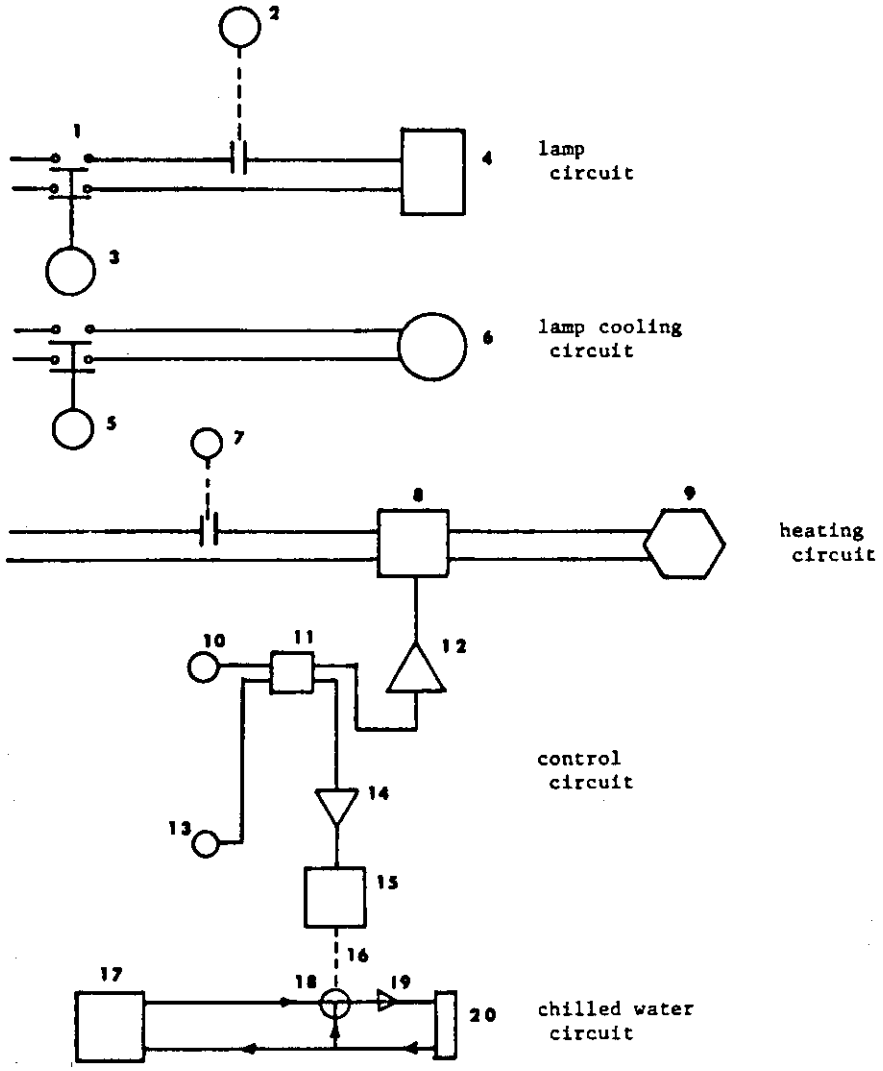

Figure 3. Control Circuits (schematic)

1. magnetic starter
2. thermostat
3. time switch
4. ballasts and lamps
5. time switch
6. fan
7. thermostat
8. SCR voltage controller
9. strip heaters
10. thermocouple
11. icepoint compensator
12. controller
13. thermocouple
14. controller
15. electropneumatic converter
16. air pressure line
17. chilled water tank
18. three-way proportional valve
19. pump
20. cooling pump

in the cooling coil.

The chilled water supply is a tank of about 150 l capacity, in which chilled water is maintained by means of a refrigeration apparatus, thermostatically controlled so as to hold a temperature several degrees below the desired temperature in coil (20). A judicious choice of the tank temperature is essential for satisfactory control of the dewpoint. With a sufficient number of plants in compartment (A), the water that is transpired is a sufficient load on the latent heat capacity of the cooling coil, so as to result in measureable drip rates and effective control. In case the transpiration load is insufficient, such as with a single small plant, a provision has been made for stream injection at point 4, using a commercial type vaporizer.

A final and significant feature of the apparatus is the control of carbon dioxide. The system is shown schematically in Figure 3. Pure carbon dioxide is taken from a high pressure cylinder through two pressure regulators. Two solenoids (4 and 5), either one of which is open, allow the carbon dioxide to be exhausted or to flow through a low volume flow meter into the plant chamber. The flow rate is set by means of low pressure regulator (3). The exhaust feature is required to prevent pulsing of the flow when solenoid (4) is turned on. The air in the growth chamber is sampled by a pump (8), at a rate of approximately 2.5 l/min and flows through the infrared carbon dioxide analyzer (Beckman 315A). The output from the analyzer is registered continuously on a strip charter recorder and is also used to drive a milliamp meter with an optical relay feature. This relay will cause the timer (12) to start on a one minute interval, whenever the CO_2 content drops below a predetermined value. In turn, the time (12) will alow the solenoid

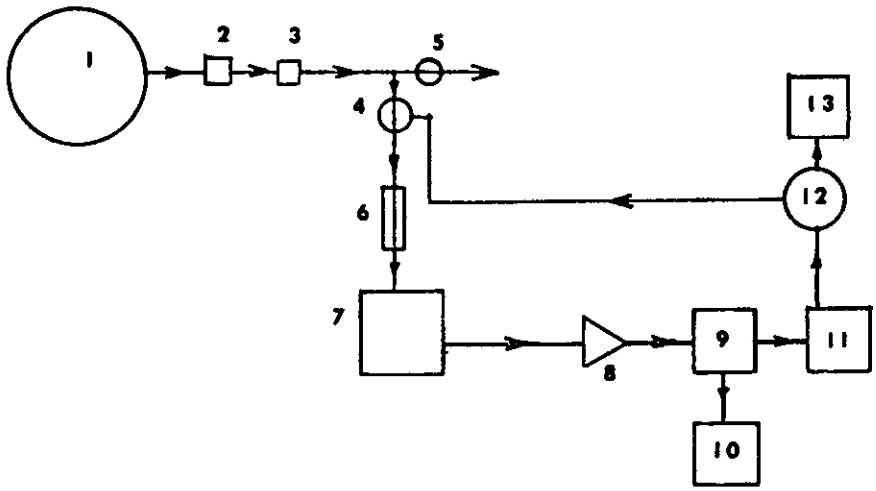

Figure 4. CO_2 Control Circuit

1. CO_2 supply
2. high pressure regulator
3. low pressure regulator
4. solenoid to plant chamber
5. exhaust solenoid
6. flow meter
7. plant chamber
8. sampling pump
9. CO_2 infrared analyzer
10. strip chart recorder
11. optical meter relay
12. timer
13. counter

(4) to be open for exactly 1 minute. The number of times that the timer (12) is activated is recorded on an electric mechanical counter (13) which can be read out by a data handling system or visually recorded. For a given time period the total amount of carbon dioxide injected follows from the flow rate, multiplied with the number of minutes of flow.

Even though the environmental simulator is made to be totally sealed, small leaks are unavoidable. The extent of the leakage can be determined experimentally without difficulty and has been found to be 215 minutes. That is to say, in 215 minutes an original differential in CO_2 content between inside and outside will be reduced to 63% of its original value. With plants in the chamber, the carbon exchange is found from the algebraic sum of the injection rate and the leakage rate. This can apply to periods to which the net photosynthesis is positive or during which it is negative. The water use follows from the rate of accumulation of water dripping from the cooling coil or it can be determined independently by weighing the entire plant or plants. With the currently used infrared analyzer it is possible to maintain carbon dioxide concentration as high as 2,000 ppm with an accuracy of approximately 1%. The calibration of the carbon dioxide analyzer itself is accomplished by precision gas mixing pumps (Wusthoff). These pumps are capable of producing CO_2-in-air mixtures, starting with pure CO_2 and CO_2-free air, with a precision of approximately .1% and as low as 90 ppm by volume.

The environmental chamber described is specified by the following performance data:

Illuminated area: 1.1 square meter

Maximum radiation flux in the photosynthetically active region: 400 watts/m^2 (with lucalox lamps, this is equivalent to about 150 kilolux or 14000 ft. candles.)

Air speed: 1.2 meters per second

Attainable temperature range: 15 to 45 °C. with a temperature control of $\pm$0.1 °C.

Control of the dewpoint: attainable with equal accuracy in the range from 12 to 45 °C., but at no time lower than 16 °C. below the air temperature. This limitation is caused by the fact that, at present, the temperature of the chilled water cannot be reduced below 11 °C.

B. Plant material and measurements.

In general, experiments consisted in growing a canopy made up by a number of plants in the environmental simulator and in measuring the CO_2 fixation by a "make up" procedure and the transpiration rate by direct weighing, or by measuring the condensate on the cooling coil. Plants were raised in the laboratory under a fluorescent light bank and moved in the simulator when sufficiently large.

Measurements made on the plants varied, but usually comprised periodic measurements of leaf resistance with the Van Bavel (1965) porometer and of leaf temperature by means of thermocouples or with a Barnes infrared thermometer. Light levels were measured with a Kipp pyranometer with a suitable filter, as suggested by McCree (1966). The light level could be varied in the simulator by the use of one or more layers of window screening immediately under the lamp barrier.

The following experiments, results of which will be given

in the following section, were carried out.

Test	Plants	Light	Air Temp.	Humidity rh. abs.
1	soybeans	400 W/m^2	25°C	.75 = 17.4 g/m^3
2	soybeans	400 W/m^2	35°C	.75 = 29.9 g/m^3
3	soybeans	400 W/m^2	16°C	.71 = 9.7 g/m^3
4	soybeans	400 W/m^2	25°C	.84 = 19.3 g/m^2
5	soybeans	400 W/m^2	35°C	.55 = 21.8 g/m^3
6	soybeans	130 W/m^2	15°C	.65 = 8.9 g/m^3
7	soybeans	130 W/m^2	25°C	.70 = 16.0 g/m^3
8	soybeans	130 W/m^2	35°C	.61 = 24.0 g/m^2
9	soybeans	70 W/m^2	15°C	.72 = 9.8 g/m^3
10	soybeans	70 W/m^2	25°C	.70 = 16.0 g/m^3
11	soybeans	70 W/m^2	35°C	.59 = 23.5 g/m^3
12	pepper	400 W/m^2	20°C	.71 = 12.3 g/m^3
13	pepper	400 W/m^2	30°C	.76 = 23.0 g/m^3
14	southern pea	280 W/m^2	25°C	.70 = 16.1 g/m^3

In each of the 14 experiments listed above the CO_2 level was maintained at 4 levels, close to 300, 600, 1200 and 1800 ppm, or 0.5, 1.0, 2.0 and 3.0 g/m^3. The air temperatures deviated no more than 1°C from the nominal levels given, whereas the actual value of humidity was about within 0.5 g/m^3 (dewpoint deviation .3°C) of that listed. During a specific experiment the control of temperature and humidity was about 0.2°C and 0.2 g/m^3, respectively. It may also be seen that the relative humidity did vary in a relatively narrow band, from .60 to .75, between experiments. This implies that the evaporative demand was considerably greater at the higher air temperatures.

4. EXPERIMENTAL RESULTS

A. Preliminary tests with soybeans (1 and 2.)

Tests 1 and 2 were preliminary since the transpiration loss was determined by a primitive method (beam balance) and automatic control of CO_2 was not available. Leaf temperature was measured on only a few leaves with attached thermocouples (0.05 mm or 2 mil wire). In this experiment the CO_2 level was set and then the measurements were made first at 25 C and, two or three hours later, at 35 C. In later work the procedure was to vary the CO_2 level at a given temperature since it appeared to take a shorter time for the plants to adjust to CO_2 level changes than to ambient temperature changes. Further, in this test only three levels of CO_2 were employed.

Fully grown but non-flowering soybean (Glycine Max, var.Lee) plants were grown in the environmental simulator in a manner similar to normal cultivation. The plants were grown in two trays, simulating rows, 60 cm apart. The resulting leaf area index was 6.

The light period was 16 hours of 400 W/m^2 photosynthetically active light. A summary of the results is given in Table 1.

The results are, in the main, that stomatal resistance roughly doubled as CO_2 went up from 300 to 800 ppm, but did not further increase beyond 800 ppm. This was true at 25 °C and 35 °C air temperature. The resistances were calculated as a canopy resistance from transpiration and leaf temperatures as the porometer calibration was not reliable and difficulties were experienced in its use.

The CO_2 fixation rate showed a consistent increase as expected and, thus, considerable improvement in the mass flux ratio was noted. However, the transpiration and CO_2 fixation data were sketchy and no final conclusion should be drawn from this experiment.

Table 1. Gas exchange by soybean plants in preliminary tests 1 and 2.

ALL FIGURES PER M^2

	25°C		
	300 ppm CO_2	800 ppm CO_2	1500 ppm CO_2
H_2O loss	4.6 g/min	2.2 g/min	2.1 g/min
CO_2 gain	0.053 g/min	.069 g/min	.098 g/min
ratio	0.012	0.031	0.045
resistance*	.15 s/mm	.29 s/mm	.30 s/mm
air temp. °C	25.7	25.2	25.0
leaf temp. °C	28.9	28.2	28.0
leaf hum. g/m^2	28.6	27.5	27.2
air hum. g/m^3	17.4	16.8	16.8
differential g/m^3	11.2	10.7	10.6

	35 C	
	300 ppm CO_2	800 ppm CO_2
H_2O loss	5.6 g/min	3.2 g/min
CO_2 gain	0.053 g/min	0.060 g/min
ratio	0.0095	0.0170
resistance*	.16 s/mm	.31 s/mm
air temp. °C	35.2	35.0
leaf temp. °C	38.3	38.0
leaf hum. g/m^3	47.0	46.3
air hum. g/m^3	31.8	29.7
differential g/m^3	15.2	16.6

*calculated

B. Definitive tests at full light levels with soybeans (3, 4 and 5).

Using the apparatus described above, now fully automated for the purpose of measuring both transpiration loss and CO_2 fixation, a series of observations were made with 18 soybean plants, having a leaf area index of approximately 4, in November 1969 at an ambient air temperature of 25 °C. Similarly, an experiment with 14 soybean plants, having a leaf area index of 3.5, was conducted in January 1970 at ambient air temperature of 15 °C and 35 °C.

The CO_2 levels were maintained at the following nominal levels: 300, 600, 1100, 1800 ppm. Extensive measurements of the leaf resistance were made during the November experiment at an ambient temperature of 25 °C. In this case an improved calibration of the diffusion porometer was available and results of a test of the adequacy of this measurement will be given further on.

At each level of ambient carbon dioxide measurements were carried on over a period of several hours. The plants had previously been grown in the laboratory under a light bank with an illumination of approximately 150 wm^{-2} (0.3--0.7 micron) for 16 hours each day. They were given 2 days or more to adapt to lighting and temperature conditions in the environmental simulator. A summary table of the entire experiment is given below.

Table 2. Response of soybean plants to air temperature and CO_2 level at an irradiance of 400 w m^{-2} (0.4--0.7 micron) and LAI of about 4. All results expressed per square meter-

CO_2 ppm	Air °C	CO_2 g/m^2 hr	H_2O g/m^2 hr	Leaf °C	Mass-flux ratio
300	16	1.97	146		.013
600	16	2.85	109		.026
1100	16	3.42	68		.051
1800	16	3.94	49		.081
				(28.5)	
300	25	3.63	463		.0078
600	25	5.77	354		.0162
1100	25	8.30	309		.0268
1800	25	10.08	215		.0468
				(29.6)	
300	35	1.96	1061		.0018
600	35	4.18	600		.0070
1100	35	6.22	525		.0118
1800	35	7.62	482		.0158
				(30.5)	

In this table the first horizontal row at each ambient CO_2 concentration gives the CO_2 fixation. The second row is the amount of water transpired, whereas the third horizontal row gives the ratio between the two as a percentage, or the mass flux ratio as previously referred to.

The table reveals remarkable and consistent increases in the mass flux ratio when the carbon dioxide concentration is increased from near normal levels to 1800 ppm. It is also plain that this increase is not a diminishing one, but that over the range examined a near linear response prevails. This is brought out in Figure 5, which shows that from the lowest to the highest concentration the increase in efficiency is 6 to 8-fold.

These findings make it possible to expect that with the proper environmental control, 10-fold increases in water use efficiency are obtainable with soybean plants. It is also obvious that the greatest efficiencies are obtainable at the lowest temperatures. This, of course, reflects principally the exponential relation between saturation vapor pressure and temperature and it can be somewhat misleading in that at the lowest temperature the carbon fixation rates were also low.

In evaluating the above data from a physical and physiological viewpoint, it must be remembered that the leaf temperatures can be expected to be considerably different from the air temperatures. In this case, where the ambient humidities were relatively high and the radiation load also high, leaf temperatures tended to be considerably above ambient. The average leaf temperature in each experiment is given in Table 2. They are about 5 °C above the air temperature.

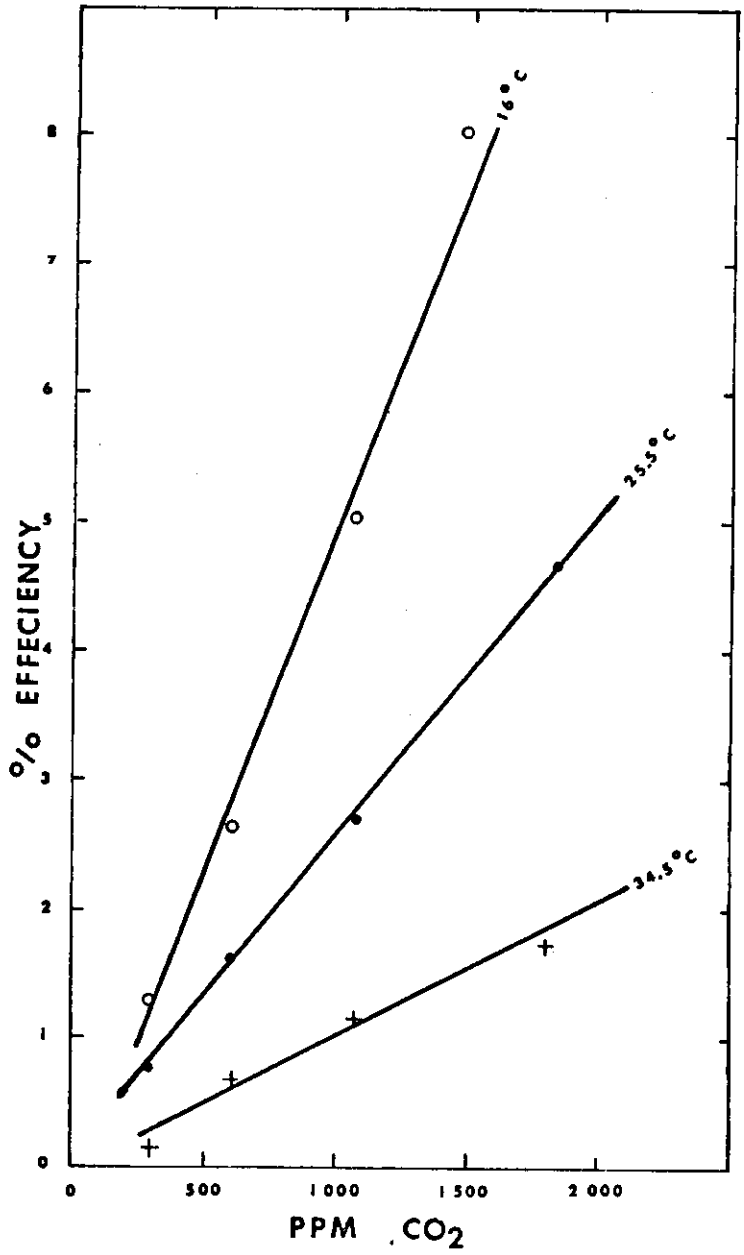

Figure 5. Effect on water use efficiency in soybeans of ambient CO_2 at three temperatures.

Within the different CO_2 levels leaf temperatures are also different as one must expect. (To illustrate this, the actual leaf temperature at each CO_2 concentration is given for the 25°C air temperature.) This spread in values is only 2°C.

The explanation of the decreased transpiration is in the progressive closure of the stomata as the CO_2 concentration increases. To investigate this independently, extensive measurements of the leaf resistance of both upper and lower epidermis were made in the case of the 25°C experiments. The values were summarized as harmonic means of all the measurements, for the reason that the individual leaf and leaf sides act as parallel resistors in the flow path of the water vapor. These values, expressed in seconds per millimeter, can be seen in Table 3 for each actual level of carbon dioxide.

Table 3. Resistances in soybean canopy at 25°C and at 4 ambient CO_2 levels.

$[CO_2]$	canopy calculated	upper leaves measured
ppm	sec mm^{-1}	sec mm^{-1}
315	.25	.26
610	.39	.50
1100	.45	.52
1820	.74	.67

The total resistance of the aggregate canopy can be calculated by an independent method, namely by dividing the transpiration per unit leaf area into the vapor pressure differential between the leaf and the ambient air. For this calculation the leaf temperature must be known. The resistance value so calculated is also given in the table and it

may be seen that the two values agree closely, in view of the fact that the external aerodynamic resistance can only have been a small fraction of a second per millimeter. Under the experimental conditions the air speed was 1.2 m/sec and a considerable amount of canopy flow must have taken place. The agreement between two sets of figures is principally a confirmation of the absolute accuracy of the leaf resistance measured by a porometer method and it confirms the method by which it was calibrated.

Together with an increase in CO_2 concentration, the resistance of the leaf to the influx of carbon dioxide increases in direct proportion to the leaf resistance to transpiration. In spite of stomatal closure, we can see in Table 2 that the absolute fixation rate increased as the consequence of the fact that the CO_2 differential across the stomata increased by a greater proportion than the stomatal resistance.

C. Test with soybeans at low light level (9, 10, and 11).

As indicated on page 13, tests at reduced levels of light were made at 130 and at 70 W/m^2 PAR (photosynthetically active radiation). The results at 130 W/m^2 were not distinctively different from those at 70 W/m^2 and will not be further reported here. The 70 W/m^2 PAR tests were carried out with 12 plants forming a canopy with a leaf area index of about 3.3.

Extensive measurements were carried out on leaf temperature using a Barnes radiothermometer. Also, leaf resistance was measured on 10 fully illuminated leaves, both top and bottom of each leaf. The results are reported as a harmonic average of the readings. Carbon dioxide fixation and water loss were determined as before. Table 4 summarizes the actual test conditions and the results. Similar to the

Table 4. Test conditions and results of gas exchange tests of a soybean canopy. Also, leaf temperature and resistance.

CO_2	Air		CO_2	H_2O	Leaf		Mass-flux
ppm	°C	g/m^3	g/m^2 hr	g/m^2 hr	°C	s/mm	ratio
300	15.1	9.8	3.12	62.0	17.4	.51	.050
600	15.2	9.8	3.05	57.6	17.8	.86	.053
1200	15.1	9.8	2.64	49.1	18.2	.95	.054
1800	15.2	9.8	2.13	43.3	17.7	.90	.049
300	25.2	16.7	3.08	172.3	25.5	.19	.018
600	25.3	16.6	3.43	139.3	26.6	.32	.025
1200	25.3	16.6	3.94	109.8	26.9	.48	.036
1800	25.2	16.7	2.79	104.5	27.2	.60	.027
300	35.0	24.2	2.66	413.7	32.3	.16	.006
600	35.2	23.9	3.08	269.0	34.7	.41	.011
1200	35.2	22.5	3.41	190.6	36.0	.52	.017
1800	35.1	23.9	3.13	204.9	34.8	-	.015

results in full light (400 W/m^2 PAR), we can observe a progressive stomatal closure (increase in resistance) as the ambient CO_2 level is increased. In accordance therewith, the transpiration shows a declining trend, though there is little difference between the 1200 and 1800 ppm levels.

In contrast with the high light level test, the CO_2 fixation rate does not or even negatively respond to increasing ambient CO_2. It also differs little between the three levels of air temperature, suggesting that its magnitude is primarily dependent upon the available light. Computer simulation does not predict this effect of CO_2 level. For instance, at 30 °C air temperature and 18.1 g/m^3 humidity and 70 W/m^2 PAR, levels similar to those of the test, we find the following predicted values for an isolated leaf, as modeled in Appendix 1.

CO_2	g/m^2 hr
300 ppm	3.2
600 ppm	4.3
1200 ppm	4.5
1800 ppm	4.6

Although the simulation is not specifically adapted to soybeans, this should not affect the trend and the computer model simply does not predict a constant or slightly declining CO_2 fixation with increasing CO_2 level.

We may further note in Table 4 that leaf resistances tend to be higher at lower leaf temperatures, an effect well known and incorporated in the computer model. On the whole, low mass flux ratios are obtained at normal temperatures and relatively small benefits are found

when raising the ambient CO_2 level.

D. Gas exchange experiments with pepper plants. (13 and 14)

Under conditions generally similar to those prevailing in the soybean tests, an experiment was performed with a stand of 14 pepper plants (Capsicum frutescens,"California Wonder"). Plants were grown in vermiculite and watered with a modified Hoagland solution. The plants were illuminated for 16 hours each day and the light level was 350 W/m^2 PAR.

At the time of the tests the plants formed a dense canopy with a leaf area index of 4.5. Air speed over the canopy was about 1.2 m/s but inside it dropped to values around 0.2 m/s.

A CO_2 response study was done at 2 air temperatures, 20.8°C and 30.1°C. Each time a steady state was reached regarding CO_2 fixation rate and transpiration rate, leaf temperature was measured on fully illuminated leaves in the top of the canopy, using methods similar to those described before. Leaf resistance measurements were not made systematically. However, from the leaf temperatures, leaf area index, and the known transpiration rate,leaf resistance was estimated.

The experimental value of the leaf resistance behaves in close accord with the simulated values as indicated by Figure 6. The simulated value is obtained by the methods of Appendix 1, using 300 W/m^2 PAR and 25°C air temperature, a humidity of 15 g/m^3. The experimental value pertains to the 30°C experiment and for this and several other reasons, we may not expect an agreement on the absolute values. However the correlation,which is in this case a similarity in changes due to CO_2 enrichment, is quite close.

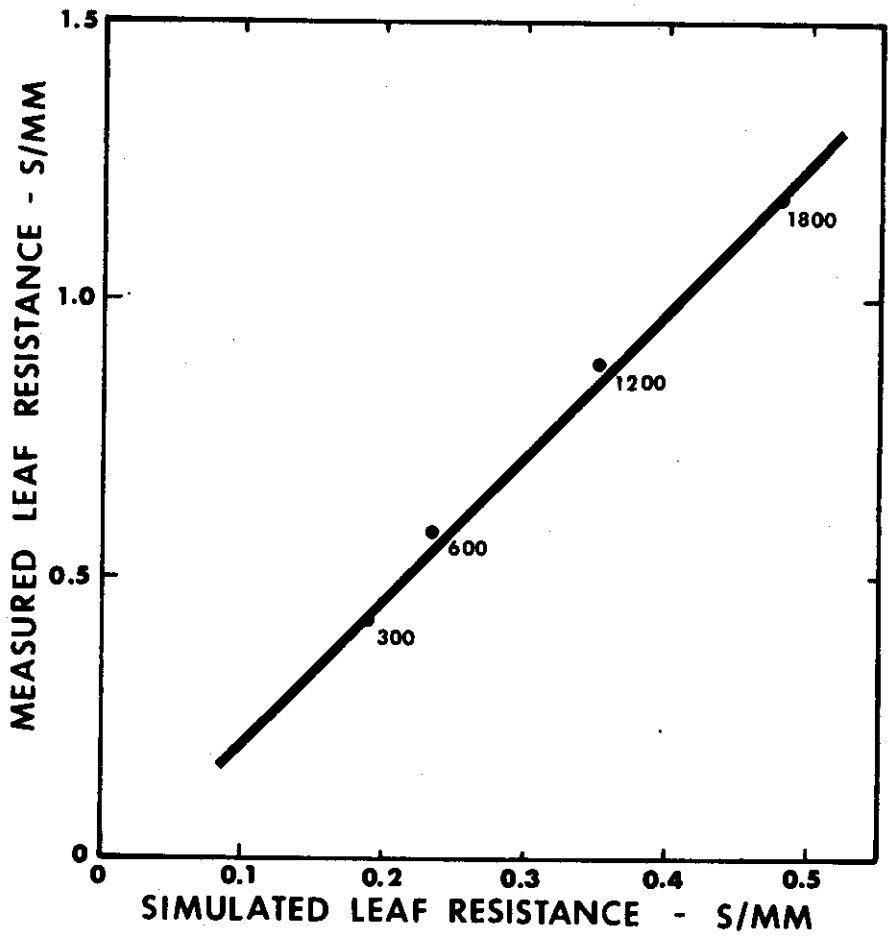

Figure 6. Measured vs. simulated leaf resistance in pepper at various ambient CO_2 levels in ppm.

Table 5 summarizes the results, which are very similar to those obtained with soybeans. The mass flux ratio shows a consistent increase at either temperature with increasing CO_2 level. Leaf temperatures and leaf resistance (as calculated) increase also as the ambient CO_2 level is increased.

A close relation is also found between measured and simulated mass flux ratios at different levels of CO_2 and at 30°C air temperature as shown in Figure 7. Comparisons such as in figure 6 and 7 are encouraging,but not final proof of any model,or premise upon which it is based. This would require specific simulation and comprehensive tests outside the scope of this report.

Table 5. Test conditons and results of gas exchange tests of a pepper canopy. Also, leaf temperatures and resistance.

CO_2	Air		CO_2	H_2O	Leaf		mass flux
ppm	°C	g/m^3	g/m^2 hr	g/m^2 hr	°C	s/mm	ratio
300	20.8	12.6	5.00	308	26.3	.62	.016
600	20.8	12.6	6.82	270	27.3	.79	.025
1200	20.8	12.6	7.03	194	28.2	1.22	.036
1800	20.8	12.6	8.24	196	28.1	1.21	.042
300	30.1	23.2	4.41	478	33.1	.43	.009
600	30.1	23.2	6.52	426	-	.59	.015
1200	30.1	23.2	7.90	348	36.0	.89	.023
1800	30.1	23.2	7.38	312	37.5	1.19	.024

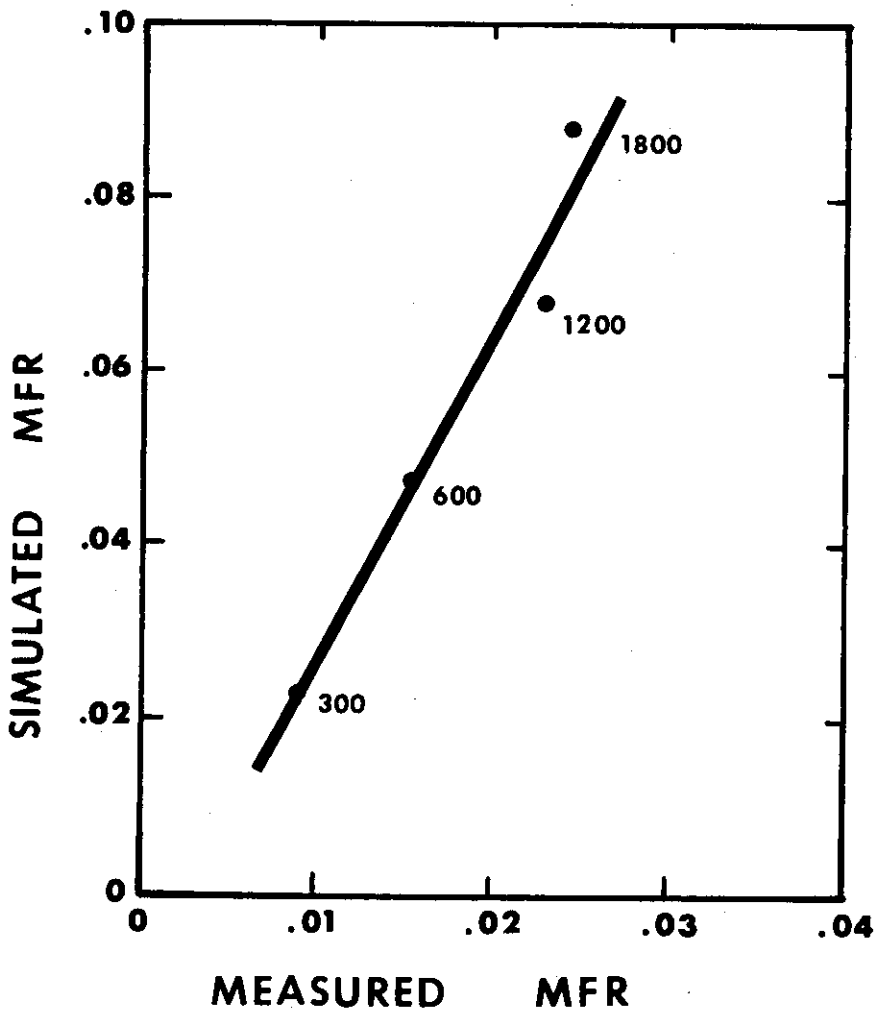

Figure 7. Measured vs. simulated mass flux ratio for pepper at various ambient CO_2 levels in ppm.

E. Gas exchange experiments with southern pea plants. (14)

A single experiment was carried out with a canopy of 18 southern pea plants (Vigna unguiculata, var. Burgundy Purple Hull). The plants were 4 weeks old at the time of the test and the canopy had a LAI of 1.12 - considerably less than the previous tests with soybeans and pepper. Southern peas have, presumably, a more sensitive stomatal guard cell compared with the two other crops used. Water deficits result easily in stomatal closure.

The plants were grown under 280 W/m^2 PAR, an air temperature of about 25°C and a vapor density of 16 g/m^3. Methods of measurement were identical to those in other tests. Leaf resistance measurements were made systematically.

Results of the test are given in Table 6, which shows that the stomata on both the upper and lower side of the leaves are sensitive to the CO_2 level but not markedly more so than in the other two crops examined. Along with this progressive closure, transpiration decreases as expected, but the CO_2 fixation rate shows an unexpected decline at the highest concentration.

Our model does not predict any such effect, which was also noted at the 1800 ppm CO_2 level with soybeans under low light (70 W/m^2 PAR). Aside from the plant response at 1800 ppm CO_2, the behavior of southern peas is similar to that of the other two crops with a sevenfold increase in mass flux ratio associated with a fourfold increase in ambient CO_2 level.

Table 6. Test conditions and results of gas exchange tests of a southern pea canopy. Also, leaf temperatures and resistances.

CO_2	Air		CO_2	H_2O	Leaf	upper/lower		mass flux
ppm	°C	g/m^3	g/m^2 hr	g/m^2 hr	°C	s/mm	s/mm	ratio
300	25.0	16.1	1.11	97.11	29.2	.50	.28	.011
600	25.0	15.9	3.05	59.04	34.0	.74	.38	.052
1200	25.0	15.8	3.92	45.53	32.7	.64	.43	.086
1800	25.0	15.8	2.24	38.77	34.0	.92	.78	.058

5. DISCUSSION AND CONCLUSION

In general, the theoretical analysis and the experimental data have shown that CO_2 is an ideal antitranspirant. By CO_2 enrichment several fold over the ambient level, partial stomatal closure can be induced. The increases in leaf diffusion resistance are not spectacular, but are approximately proportional to the ambient CO_2 level. At the same time the assimilation rate of the plants is increased by CO_2 enrichment according to a general law of diminishing returns. Little, or even in some cases, a negative effect is noted at ambient levels over 1200 ppm.

All these responses depend upon other factors: light, air temperature and humidity. The theoretical model is primarily intended to predict and summarize all these influences. Some of the experimental data can be used to check the model predictions and these tests corroborate the theory fairly well. But, a notable exception is the failure of the model to suggest that at high CO_2 levels, its fixation may be reduced. This point should be examined further in experiments as well as in theory. An experimental oversight or misinterpretation is not impossible.

A weakness in the experimental procedure has been the measurement of leaf resistance. Since this work was done, the procedures for measurement and calibration have been improved considerably.

As we have established a reasonable basis for expecting significant increases in water use efficiency by plants through CO_2 enrichment, we may well ask what the possible practical implications are. To do any good, CO_2 levels must be raised considerably and, under

field conditions, this implies very high release rates of CO_2. Although the theory has not been worked out completely, it is apparent that in order to maintain, say, a level of 1000 ppm CO_2 in a field crop, the release rate at the soil surface may have to be as high as 500 kg per ha and per hour. On the basis of our own results the rate of CO_2 fixation could hardly be more than 50 kg per ha and per hour, and in the field this may be less. Thus a capture of 5% of the CO_2 released is about as much as can be expected. Water use under such a condition may be reduced by 50% and growth rate could easily double. Yet, the plausible economics of CO_2 release are not encouraging the detailed pursuit of field application.

A different picture exists regarding enclosures such as glass houses, domes, plastic tunnels and the like. In these, virtually complete capture could be achieved and transpiration cut down. Of course, humidification could achieve the latter as well, and it has been suggested that research on the combination of two practices is what is really needed. The simulation work that has come out of this project, strongly suggests this synergism also, leading to a very high value-in-use of water that could justify such water resources as desalting sea or brackish water.

6. SUMMARY

In this report we have critically examined the proposition that enrichment with CO_2 of the air surrounding plants may, simultaneously, enhance their growth and decrease their water use.

Analysis of the mechanisms involved pointed out the need for a stomatal action hypothesis and we have postulated that leaf stomatal resistance is directly proportional to the internal carbon dioxide level of the leaf and to the exponential of the leaf water potential (absolute value). With this and other commonly used ground-rules of leaf behavior we have made up a simulation model of leaf action that was used to explore the CO_2 effect, as noted above, in considerable detail. The simulation confirmed the notion that CO_2 should be regarded as an ideal antitranspirant.

A series of experiments was performed with small stands of soybeans, peppers and southern peas. These were done in an artificial and controlled environment that simulated typical outdoor conditions by having equally high light levels, air movement and evaporative demand. Increasing CO_2 levels from 300 up to 1800 ppm gave increased stomatal resistance, decreased transpiration, higher leaf temperatures, increased carbon dioxide assimilation, and, in consequence a greatly increased mass flux ratio between carbon dioxide and water vapor.

Qualitatively and quantitatively the results agree with the theory with some exception at the highest CO_2 levels tested. However, the experiments were only a partial and inconclusive test of the model and additional experimental studies are indicated.

The practical implication of this work are unclear. In the

field the limited capture efficiency of released CO_2 and the large quantities needed to have the desired effect, are not encouraging. In enclosures the effects of CO_2 enrichment are easily understood and should lead to unusually high values-in-use of water consumed in plant production. It may be possible to operate enclosures with high CO_2 without extremely high humidities and still maintain maximum plant growth and production.

7. REFERENCES

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8. APPENDIX 1

A MODEL OF GAS AND ENERGY EXCHANGE REGULATION BY STOMATAL ACTION IN PLANT LEAVES

C. H. M. van Bavel, D. W. DeMichele and J. Ahmed

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Appendix 1

ADDITIONAL INDEX WORDS

Transpiration

Carbon dioxide assimilation

Water use efficiency

Compensation point

Stomatal sensitivity

Humidity

Carbon dioxide level

Photosynthesis

Leaf resistance

A MODEL OF GAS AND ENERGY EXCHANGE REGULATION BY STOMATAL ACTION IN PLANT LEAVES[1/]

C. H. M. van Bavel, D. W. DeMichele and J. Ahmed[2/]

INTRODUCTION

The behavior of leaf canopies regarding gas and energy exchange has been explained in terms of a single, horizontal leaf model (Penman and Schofield, 1951, Monteith, 1963). A second approach has been to consider the canopy as a multilayered assembly in which the leaf area density, as well as other physical and physiological properties depend upon the height above the ground (Lemon et.al. 1971, Uchijima, 1970).

In either case, it is generally accepted that the disposition of the stomatal apparatus is an important element in such a theory, or model. Furthermore, it is also clear, from many observations made in both field and laboratory, that the opening and closing of leaf stomata responds, simultaneously, to several factors: irradiance, ambient CO_2 level, water balance and potential, and leaf temperature. (See Meidner and Mansfield,1968, for a general review, also Ketelapper, 1963).

The stomatal resistance to diffusive flow of water vapor has been taken into account in earlier analyses of the energy and water balance of leaves (Raschke, 1962, Gates, 1968). In this work the resistance was, however, not treated as a variable that itself depended

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upon the functioning of the leaf. A step in this direction was taken by Waggoner (1969), by providing for the stomatal resistance to depend upon the level of light. This subroutine was incorporated by Waggoner (1969), in a model for the behavior of leaf canopies. This factor was also taken in consideration by Lommen, et.al. (1971) in a detailed analysis of leaf photosynthesis, emphasizing the role of enzymatically controlled processes.

It has always been held that the prime function of stomata is to regulate the leaf water balance. Yet, only recently has one model (Lommen, et.al (1971) accounted for the dependence of stomatal aperture upon the leaf water potential. It is also widely recognized that temperature affects stomatal action. However, this has not been considered in any model.

Opinions will vary as to which environmental or internal factor is the most important one in determining stomatal resistance in a given set of circumstances. An unbiased judgment - and more importantly, a correct prediction of leaf behavior - can come only from a comprehensive model, that takes all known environmental factors into account simultaneously. To do so is the purpose of the work reported here. We hope that a comprehensive theory will enable practically oriented simplifications that are not arbitrary and that can help explain and predict plant behavior.

In this analysis we observe two guidelines. One is that the emphasis should be upon considering all known factors and every interaction, rather than upon the precise definition of each individual effect. The second one is that the model should be internally consistent, that is, energy and mass must be conserved.

Wherever possible and practical, known physical and physiological laws should be used. Many physiological data can be described only in an empirical fashion and cannot be derived from the fundamental biochemical processes. For example, our model recognizes the existence of a CO_2 compensation point and demonstrates its role in gas exchange regulation, including transpiration. However, it does not reflect any of the metabolic reactions or mechanisms that are thought to be the cause of the existence of a CO_2 compensation point, or that determine its actual value. This aspect was studied in detail by Lommen, et.al. (1971).

The possible usefulness of a comprehensive leaf action model resides in two applications. First, it can be considered as an improved "subroutine" in the modeling of leaf canopy behavior under field conditions. Second, it can be used as a tool in "sensitivity analysis", in that it can be used to answer questions as to which environmental or plant characteristics are most important. For example, a model can help determine which parameters control the efficiency of light utilization in photosynthesis, or, the relation between windspeed and transpiration.

If the theory is sufficiently accurate, a matter to be decided only by experiment, it can suggest solutions of an engineering nature in either of the two applications cited above. Thus, we may be able to predict whether an increase in planting density of a crop may lead to a disadvantageous depletion of CO_2 inside a canopy. Such a prediction will also require a model of gas exchange in the canopy, as suggested by Waggoner (1969b) and by Uchijima (1970), and one of light penetration. Or, the relative merit of varietal differences in

stomatal density, or sensitivity to water stress can be analyzed by simulation in preparation for comparative field and laboratory tests with crop plants.

MODEL CONSTRUCTION AND DERIVATION

For the present purpose a single leaf is considered as an internally homogeneous body, contained within a perforated epidermis on both sides. Further, both leaf temperature (TL) and the internal (interstitial) carbon dioxide density (CL) are assumed to be the same throughout. Both are dependent variables, as is the leaf water potential (WPOT). The latter is an indicator of the balance between water supply and water loss by transpiration. One distinctive feature of the model is that the stomatal resistance for diffusion for the upper surface (RLU) and the lower one (RLL), respectively, depend upon leaf temperature, leaf carbon dioxide level and leaf water potential, as discussed in detail later on.

The principle of internal continuity is represented by three conservation equations. The first one is the energy balance of the leaf in which LR is the black body radiation emanating from the leaf, LE the latent heat of transpiration, SE the sensible heat exchange between leaf and air, and TR the total radiant load absorbed:

$$LR + SE + LE + TR = 0 \qquad (1)$$

Note that the energy equivalent of photosynthesis is neglected, although it could be incorporated in the model without difficulty.

The second equation is the carbon balance or net photosynthesis (NP) of the leaf which states the equality of NP to the diffusive flow of CO_2 into the leaf:

$$NP = (CA - CL)/RTOTC \qquad (2)$$

and in which CA is the external level of CO_2. RTOTC is the harmonic mean of upper and lower surface resistance; divided by 2:

$$RTOTC = 1/(1/(1.53 * RLU + RA) + 1/(1.53 * RLL + RA)) \quad (3)$$

RA being the boundary layer resistance. The number 1.53 expresses the difference in diffusion rates between water vapor and carbon dioxide. The value for NP, to be discussed later, is determined by internal functions and conditions.

The third equation is that of the water balance of the leaf; and expresses the equality of the water uptake to the transpiration:

$$WPOT/SRPL = (HA - HL)/RTOT \quad (4)$$

in which HA and HL are the absolute humidities in the air and in the leaf, respectively. The water potential in the leaf (WPOT) is the driving force for the transpiration stream provided we assume a root medium potential of zero. SRPL is the resistance for liquid flow in the plant, expressed on a unit leaf area basis, or the "specific resistance of the plant". We further assume that this resistance is constant, though this has been questioned by some (Barrs, 1970). The value of RTOT is given again by the harmonic mean; divided by 2:

$$RTOT = 1/(1/(RLU + RA) + 1/(RLL + RA)) \quad (5)$$

The form of (3) and (5) implies that the value of RA is taken to be identical for either side of the leaf. Also, it is assumed that RA has the same value for the transport of sensible heat, water vapor and carbon dioxide.

Equations (1), (2) and (4) are, in essence, the model. The anticipated behavior of the leaf follows from the requirement that a set of values for TL, CL, and WPOT must satisfy all three relations, when all other external conditions and plant properties are specified.

But, in order to proceed with a numerical solution, a number of auxiliary relations must be stated, or assumed.

The value of RA is specified by a commonly accepted expression (Thom, 1968) for a leaf that is edgewise exposed to the air flow:

$$RA = 252 / \sqrt{SA/LL} \quad s/m \tag{6}$$

provided SA is expressed in m/s and LL in m. The following relations apply to the terms of the energy balance:

$$LE = LH * (HA - HL)/RTOT \quad W/m^2 \tag{7}$$

LH being the latent heat of vaporization (2442 J/g). Also obvious are:

$$SE = 2 * SH * (TA - TL)/RA \quad W/m^2 \tag{8}$$

in which SH is the specific heat of air per unit volume (1005 J/deg m^3)m and:

$$LR = 2*5.67*10^{-8}*TL^4 \quad W/m^2 \tag{9}$$

the usual blackbody radiation expression. A factor of 2 is required in equations (8) and (9) to account for the two surfaces of the leaf. Also needed is an expression relating the total absorbed radiation to the photosynthetically active radiation (PR). From a number of literature data, including spectral absorbtance of leaves, the following expression seems to represent the radiation absorbed by a leaf horizontally exposed to a bright, daytime sky over a moist soil surface:

$$TR = 700 + 1.3 * PR \quad W/m^2 \tag{10}*$$

This expression accounts for both sides of the leaf. Additional detail is supplied in Addendum I. Finally, the relation between TL and HL is specified by the Goff-Gratch equation (List, 1966). We have used a numerically simpler form, as given by Murray (1967):

$$HL = 1323 \text{ EXP } (17.269 \text{ TL}/(237.3 + \text{TL}))/(273.16 + \text{TL})$$

*/ An improved form of this equation is discussed in Addendum I also.

To this point we have been describing the transport phenomena and the energy balance in a standard fashion. Now we must consider the processes that are biochemical in nature, and in doing so we must be largely empirical. First, we must describe the dependence of NP upon the internal parameters, TL and CL, and upon PR, the absorbed light energy. To do so requires a specification of the maximum rate of gross photosynthesis the leaf structure is capable of sustaining (NPMAX). Further, it requires consideration of the compensation point for CO_2 (COMP), being the minimum external CO_2 level that the leaf can induce. It is necessary to include constants (K1 and K2) that described the "saturation" of the photosynthetic process with CO_2 (internal) and light, respectively. Also, it is required to build in an appropriate biological temperature response (FCNT) that has a minimum, an optimum, and a maximum. Finally, the existence of a basal or maintenance (dark) respiration must be recognized (DRESP). To accomplish this, we have used the following equation:

$$NP = (NPMAX*(EXP(-K1*COMP)-EXP(-K1*CL))*(1-EXP(-K2*PR)) -DRESP)*FCNT \quad g/m^2\ hr \qquad (11)$$

The form of FCNT is illustrated in Figure 1. Assuming a value of 5 (m^3/g) for K1 and of 0.01(m^2/W) for K2, the two exponential saturation curves are also shown in Figure 1. The CO_2 response is illustrated for two values of the CO_2 compensation point. Note that the CO_2 curves are in terms of <u>internal</u> CO_2 concentration, and that they apply for light saturation and a leaf temperature of 35 C. Similarly, the light curve applies at CO_2 saturation (internal) and 35 C.

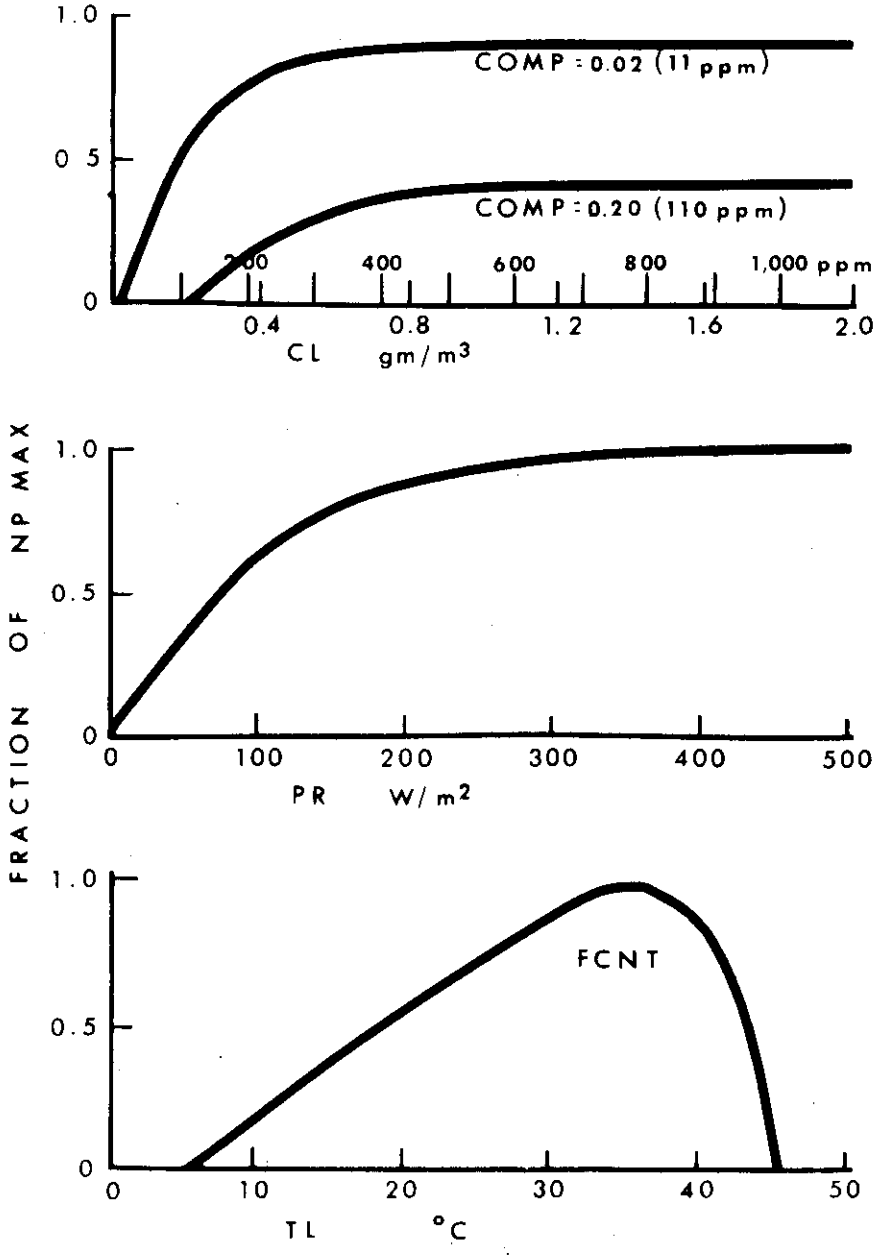

Figure 1. Illustration of the separate effects of internal CO_2 level (CL), absorbed light (PR), and leaf temperature (TL) upon net CO_2 exchange as implied by equation (11).

Other workers have preferred Michaelis-Menten expressions for the saturation curves. The precise form appears of secondary importance as long as a diminishing effect with resonable bounds can be built into the overall model. The important thing is that TL and CL are treated as dependent and interdependent variables.

There is less known about stomatal behavior and the underlying mechanisms than about photosynthesis. Accordingly, it is more hazardous to write a quantitative expression for the relative degree of aperture, in which RLU and RLL are made to depend upon CL, TL and WPOT. We have, for the time being, not distinguished between upper and lower surfaces, and considered that there is a maximum possible aperture that will result in a minimum resistance, RLMIN. The actual value of RL will be greater at suboptimal temperatures; also it will be greater as the internal CO_2 level becomes greater. Finally, RL is quite sensitive to the water potential in such a way that at a sufficiently low value of WPOT almost complete closure results. Nevertheless, under no condition will RL be infinite, since cuticular diffusion will always allow a finite value (RLMAX).

These ideas are embodied in the following two relations:

$$RL = 1/(1/RLS + 1/RLMAX) \qquad (12)$$

in which:

$$RLS = RLMIN*(1+K3*CL)*EXP(-SENS*WPOT)/ERFC(TL/TLMIN) \qquad (13)$$

in which ERFC is the complementary error function.

The functional form of this set of two equations is illustrated in Figure 2, in which we assumed that RLMIN would be 10 s/m, RLMAX 10,000 s/m, K3 10.0 m^3/g, and TLMIN 30 C. Three values were employed for SENS: 0.1, 0.3, and 1.0 bar^{-1}, demonstrating the effect

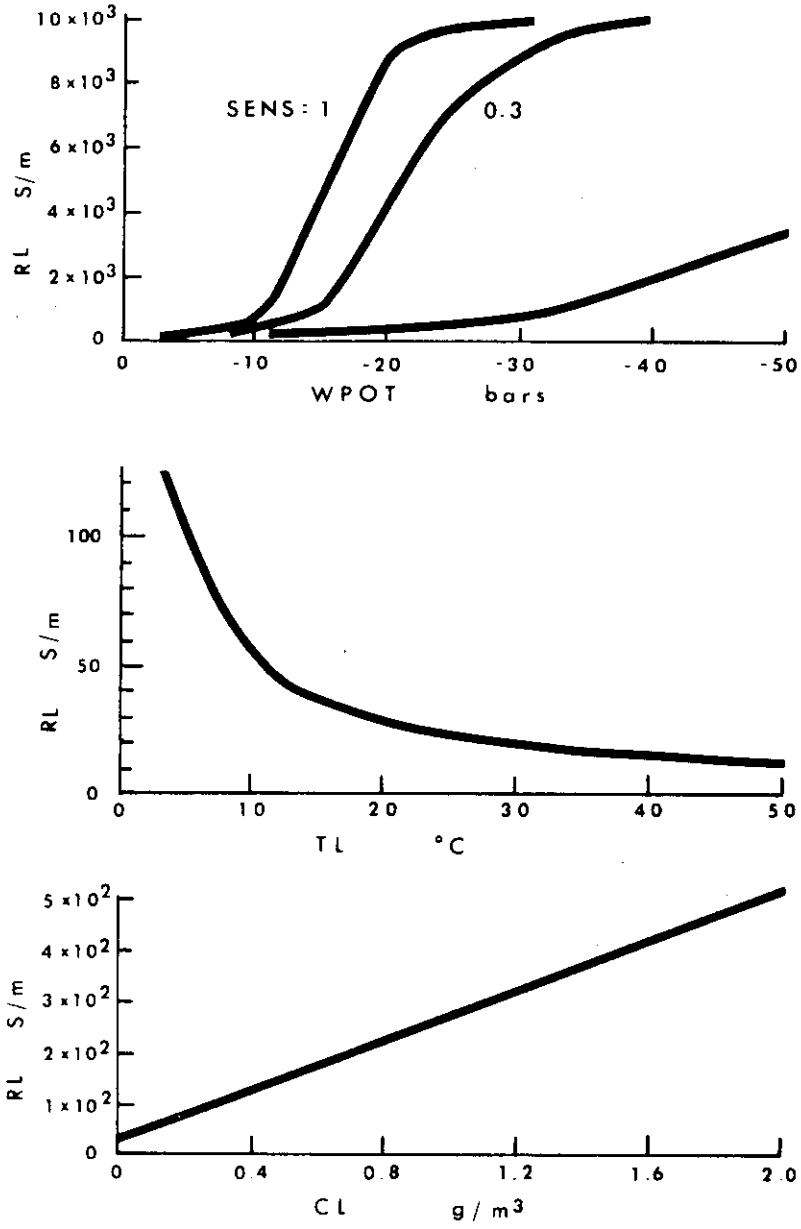

Figure 2. Illustration of the separate effects of leaf water potential (WPOT), leaf temperature (TL), and internal CO_2 level (CL) upon leaf diffusion resistance (RL), as implied by equations (12) and (13).

of different sensitivities of the stomata to the water balance. It is certain that expression (13) can be improved as additional experimental data become available, or as a more specific physiologic models of stomatal action can be built.

A diagrammatic representation of the complete model is given in Figure 3. In this schematic we have indicated 6 feedback loops, that are useful in identifying differences between this work and previous efforts. Loops 1, 2, and 3 are ordinarily recognized in energy balance models, since they derive from the leaf temperature. Loop 4, which recognizes the regulatory function of the stomata in transpiration has not been represented before except in a simple on-off form (Cowan, 1965). Loops 5 and 6, that link photosynthesis to transpiration, and light utilization to ambient CO_2 and viceversa, have not been previously incorporated in leaf action models. Figure 3 has only conceptual significance, whereas the computing routine is based upon the system of equations given before. The general set of equations were solved for various environmental conditions and plant parameters by the Newton-Rhaphson method. A digital computer program was written to solve the set of equations and automatically plot the results.

NUMERICAL INPUTS AND SPECIFICATIONS

Though some parameters have been defined before, a listing is provided here (see also the glossary), separated in two groups; leaf and plant characteristics, and environmental characteristics. For the purpose of simulation, several of these (indicated as *) have been allowed to vary step-wise. The range of variation is given.

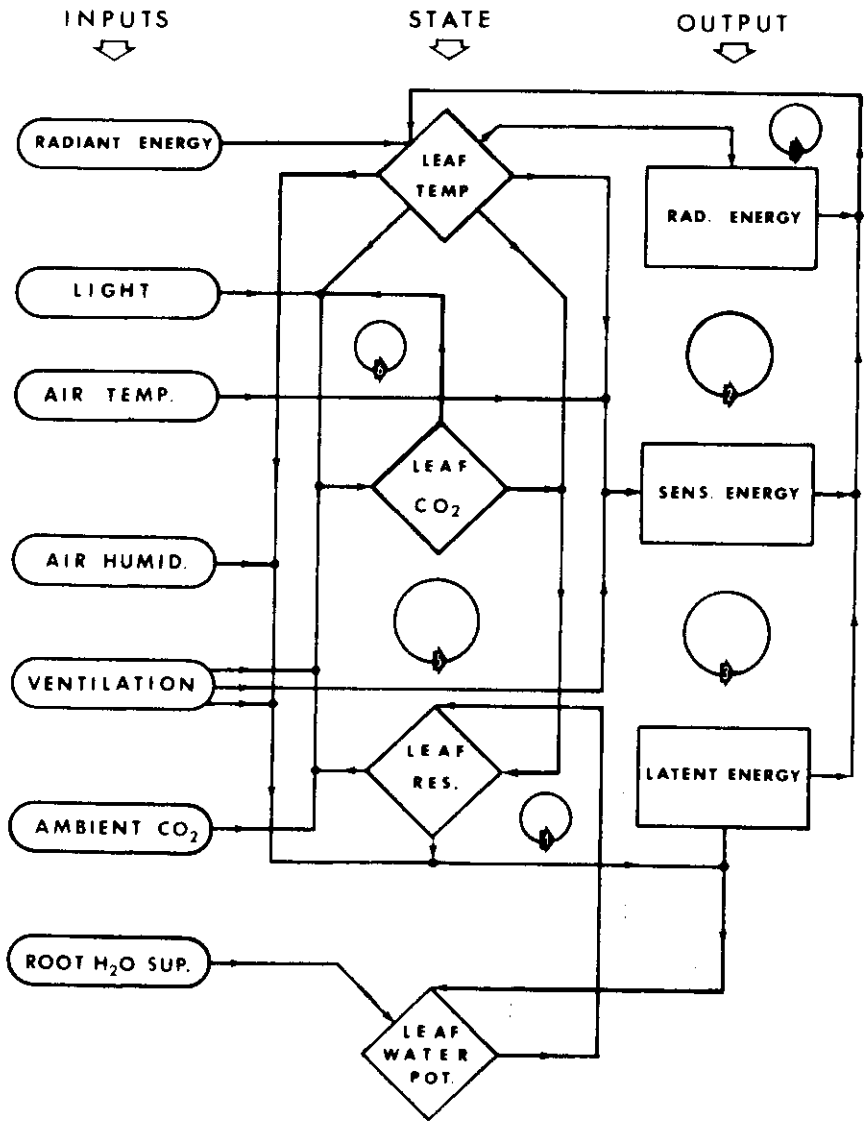

Figure 3. Illustrative diagram of the relations between input, output and state variables in the leaf action model. The feedback loops (1-6) are identified in the text.

Table 1. Plant characteristics.

variable	ref. eq. #	"typical" value	range
NPMAX	11	20 g/m^2 hr	
DRESP	11	0.5 g/m^2 hr	
*COMP	11	0.10 g/m^3	0.02-0.20
		(56 ppm)	(11 - 110)
FCNT	11	See Figure 1	
K1	11	5.0 m^3/g	
K2	11	0.01 m^2/W	
K3	13	10.0 m^3/g	
LL	6	0.05 m	
*RLMIN	13	10 s/m	10 - 100
RLMAX	12	10,000 s/m	
*SENS	13	0.3 1/bar	0.1 - 1.0
TLMIN	13	30° C	
*SRPL	4	50 bar m^2 s/g	

The last value needs comment. Few experiments have been reported in which the plant resistance to water flow was calculated and in even fewer is the leaf area given. The value given here is an estimate derived from work by Jensen (1961) and by Boyer (1971) and from data collected in our laboratory by Hailey (1971). The significance of SRPL (specific resistance of plant) is considerable as we can demonstrate from our results.

Table 2. Environmental characteristics.

variable	ref. eq. #	"typical" value	range
PR	11	300 W/m^2	0-500
TR	1,10	1090 W/m^2	700-1350
TA	8	30 °C	0-50
HA	4	18.1 g/m^3	0.5-25.0
SA	6	2.0 m/s	0.2-10.0
CA	2	0.575 g/m^3	0.105.0
		(319 ppm)	(55-2770)

In the simulation runs, each environmental input was allowed to vary over the range indicated while the others were held constant at a "typical" level, as shown. Exceptions to this were the humidity (HA) which, in the case of variable air temperature (TA), was specified as 0.60 of saturation (relative humidity), and the light level which was linked to the total radiation (TR) as implied by equation (10). Finally, since we were particularly interested in ambient CO_2 effects, simulation runs were made for 10 levels of CA from 0.5 to 5.0 g/m^3 (277 to 2770 ppm).

For additional orientation, it is noted that the "typical" value of PR is about equal to 2/3 full sunlight (direct and normal beam). TA and HA are representative of subtropical, or continental summer values for the daytime. The air speed is a median value and CA was set close to the current global value.

Further, regarding the plant characteristics, the "typical" values of DRESP and NPMAX were estimated from the literature, as were FCNT, K1 and K2. The assumed "typical" value of COMP is found, in many plants having the Calvin or C3 cycle of photosynthesis. The

number chosen for RLMIN typifies a leaf endowed with numerous and large stomata on either side.

SIMULATION RESULTS

Temperature effects.

Although air temperature is not necessarily the most incisive factor influencing leaf behavior, it is usually of the widest interest to agronomists and the single parameter most likely measured in crop physiology. Thus we illustrate the action of the model by taking air temperature as an environmental variable, together with three variable plant parameters: compensation point, stomatal sensitivity to leaf water potential, and minimum stomatal resistance. Considering the implication of both Figures 1 and 2, it must be obvious that one cannot speak of a given "relation between photosynthesis and air temperature", for example. There are an infinite number of such and all we can do is illustrate the range of possibilities.

In Figure 4 the effect is shown of ambient air temperature upon net photosynthesis for 10 levels of the compensation point. The other environmental and plant parameters are those cited in Table 2. While the importance of the compensation point for the level of net CO_2 fixation is obvious, one can also see that the temperature effect is not the same in each curve. Low-compensation point plants are more sensitive to ambient temperature. In all cases, the maximum occurs at about 39 °C air temperature, 4 degrees above the temperature at which the maximum leaf activity was taken to occur (see FCNT, Figure 1). This effect is principally caused by the transpirational cooling.

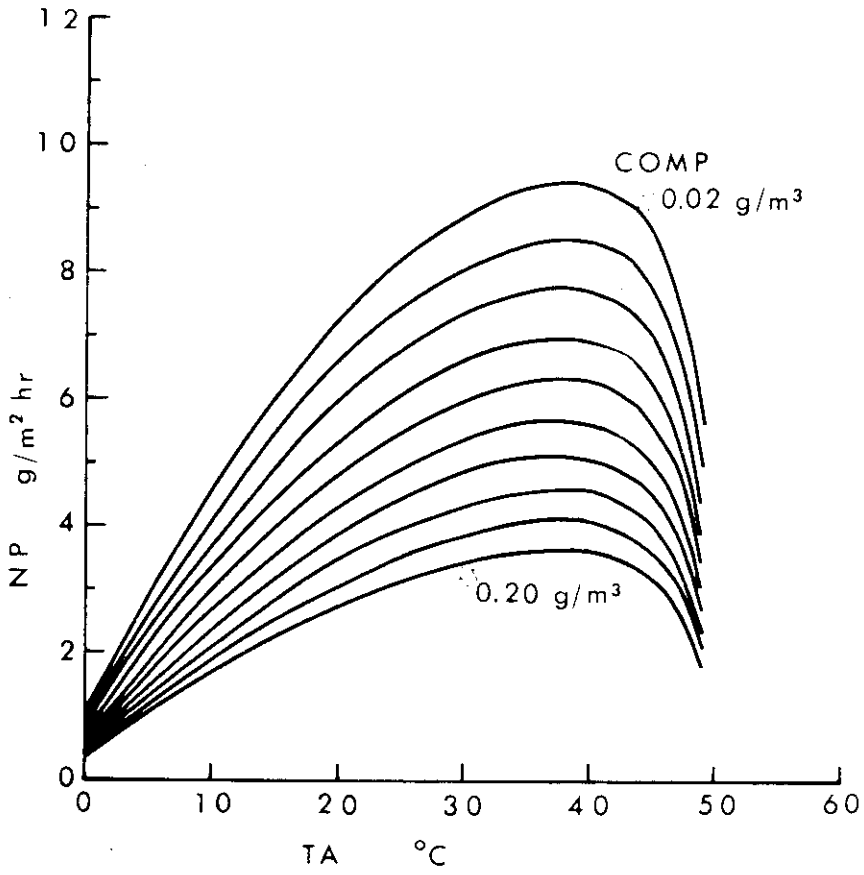

Figure 4. Calculated relation between net carbon dioxide exchange in g/m^2 hr and ambient temperature for different values of the CO_2 compensation point in steps of 0.02 g/m^3. All other conditions as in Tables 1 and 2.

A quite different response is obtained when we allow the stomatal sensitivity to leaf water potential to vary (refer also to Figure 2, top). Figure 5 shows a reduction in net photosynthesis primarily related to the stomatal closure induced by transpiration. The effect of the increase in transpiration with increasing temperature varies with stomatal sensitivity. In a sensitive leaf (bottom curve), the net CO_2 exchange reaches a maximum at 25 °C and exhibits a near-flat reponse. Such a behavior could explain midday depression of photosynthesis, even if soil water supplies were ample. On the other hand, a non-sensitive leaf, exemplified by crops such as cotton or sorghum, shows a maximum photosynthesis rate at ambient air temperatures of 40 °C and higher. Again, this air temperature exceeds the optimum leaf temperature. So-called temperature adaptation may well reside to a large extent in the response of leaf stomata to leaf drying, by maintaining high transpiration and cooling rates.

A third type of effect is associated with the number and/or size of the stomata, as represented by the parameter RLMIN. Figure 6 shows that the overall efficiency of the leaf in fixing CO_2 is definitely influenced by the value of this stomatal parameter, but that the effect of air temperature is about the same. In considering this response we must remember that the "typical" air speed used was 2 m/s and that, therefore, the model leaf was well ventilated, though in a manner not uncommon for an open field situation. For the leaf dimensions used here, the value of RA (the boundary layer resistance) was 39 s/m. At a relatively low air speed of 0.4 m/s, RA would be 89 s/m. Even this value is low compared to the "typical" value of RL, (the leaf resistance) which, for the standard conditions, is

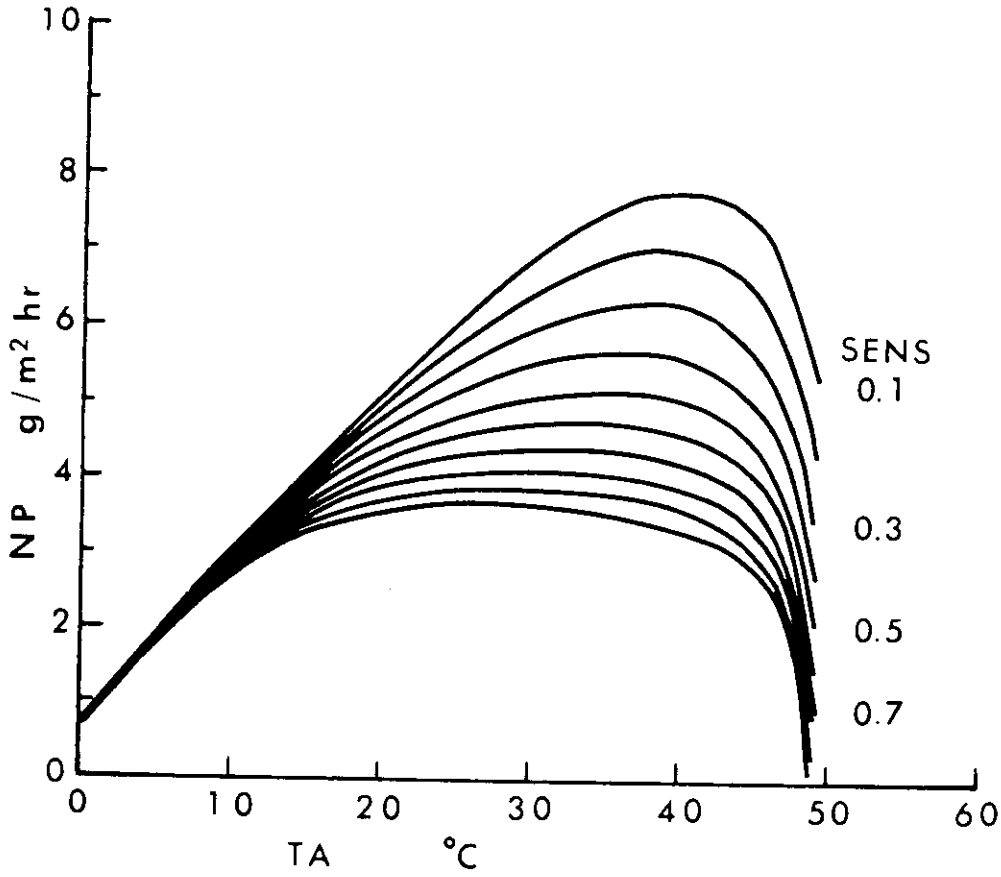

Figure 5. Calculated relation between net carbon dioxide exchange in g/m^2 hr and ambient temperature for different values of stomatal sensitivity to leaf water potential. All other conditions as in Tables 1 and 2.

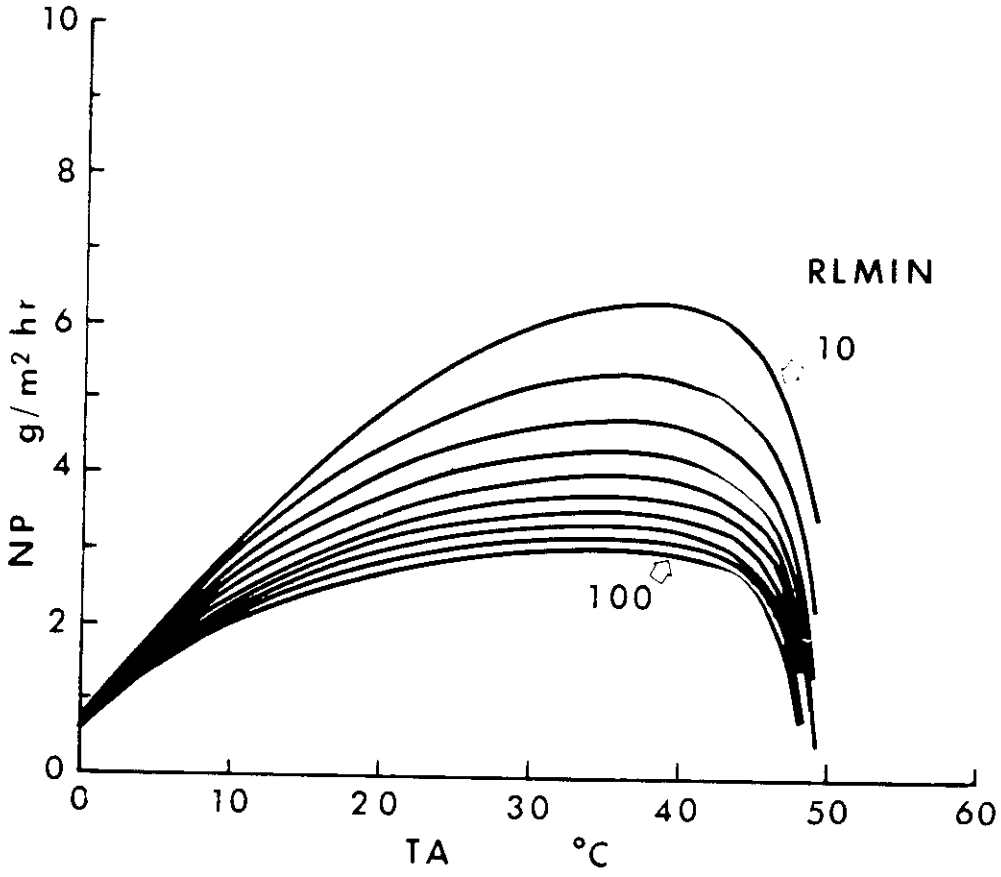

Figure 6. Calculated relation between net carbon dioxide exchange in g/m^2 hr and ambient temperature for different values of the minimal stomatal resistance. All other conditions as in Tables 1 and 2.

154 s/m. Thus, stomatal resistance still dominates in the "average" situation in which TL = 28.3 °C, or 1.7 °C below ambient air temperature. The leaf water potential is -8.9 bar, and the transpiration rate equivalent to an energy flux of 190 W/m^2 (0.27 ly/min), or 270 g/m^2 hr.

Wind effects

In artificial environments, such as plant growth chambers, air speeds are often unrealistically low (Van Bavel, 1971 and Gaastra, 1971). A mistaken notion of the effect of air speed upon gas exchange can arise from observations made under such conditions. In the outdoors, when air speeds are 0.5 m/s and up, changes in windspeed do not have a large effect on plant response as one may see from the simulation of its effect on net CO_2 exchange and transpiration in Figure 7. However, if stomatal resistance is quite low this effect could be more pronounced, as several other investigations have demonstrated before.

Because of air speed chosen for the simulations, the sensible heat exchange between leaf and air is vigorous and differences between leaf and air temperature are not large. This effect is illustrated in Figure 8 showing the relation between leaf temperature and air temperature for different stomatal sensitivities to leaf water potential. At low air temperatures leaf temperatures tend to be several degrees higher, and at high air temperatures they are lower. Air temperature and leaf temperature are about equal at 28 °C, depending somewhat upon stomatal sensitivity. This result agrees well with Linacre's survey study (1964). The precise leaf temperature value will depend in each case upon the transpiration-a point stressed earlier by Gates (1968). Yet, in the overall energy balance of the

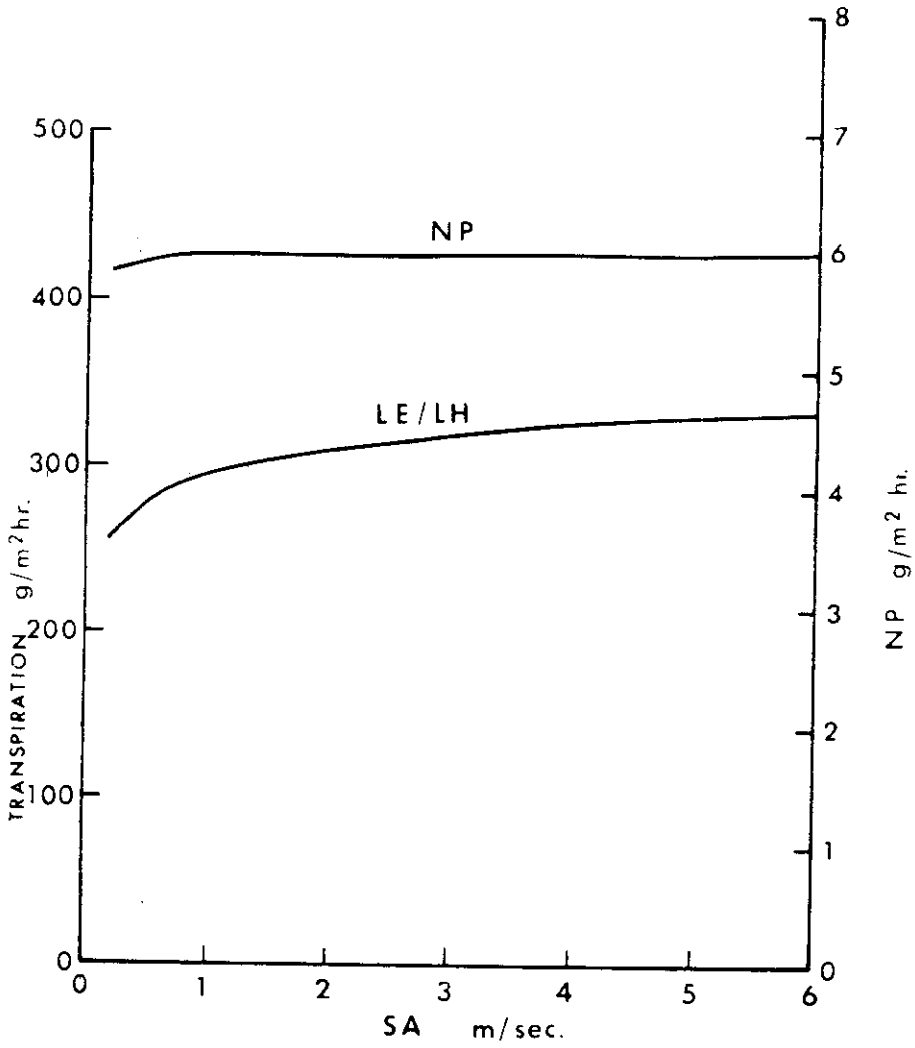

Figure 7. Calculated relation between net carbon dioxide exchange (NP) in g/m^2 hr and air speed in m/s. Also, between transpiration (LE/LH) in g/m^2 hr and air speed. All other conditions as in Tables 1 and 2.

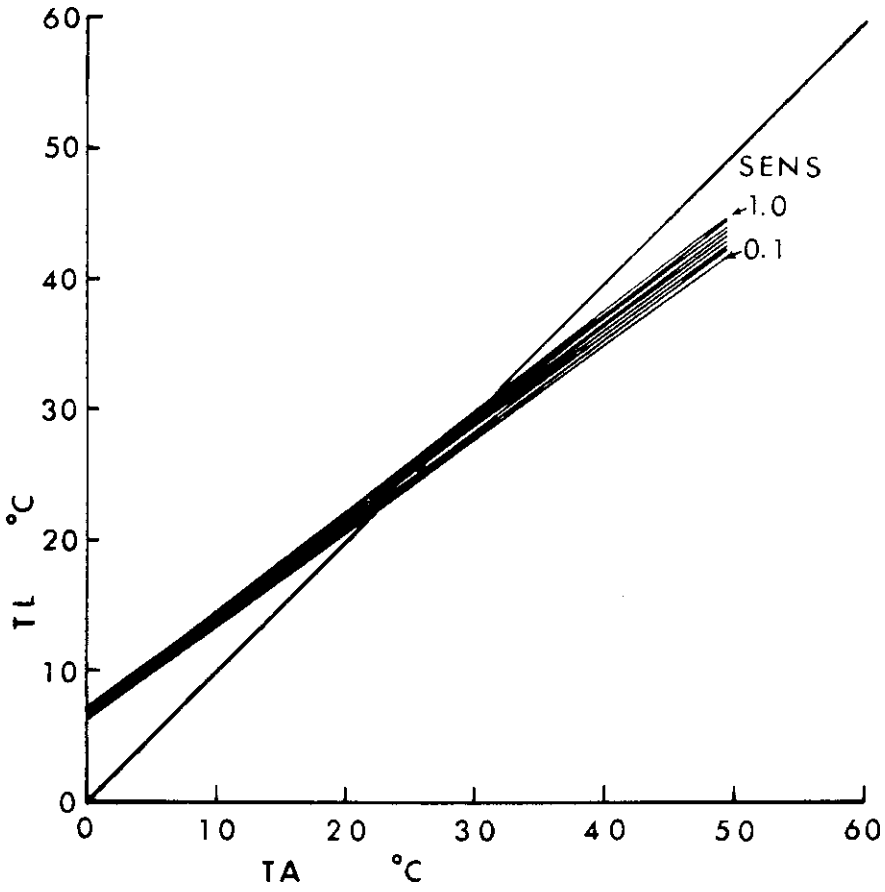

Figure 8. Calculated relation between leaf temperature (TL) and air temperature (TA) for different values of stomatal sensitivity to leaf water potential. All other conditions as in Tables 1 and 2. The single solid line indicates equality of temperature.

leaf, the blackbody radiation (LR) will always be the dominant term. For instance, at 29 °C air temperature and for a stomatal sensitivity of 0.3 we obtain:

LE = -215 W/m^2 = -0.31 ly/min

SE = +56 W/m^2 = +0.08 ly/min

LR = -931 W/m^2 = -1.33 ly/min

TR = +1090 W/m^2 = 1.56 ly/min

RL = 182 s/m = 1.8 s/cm

(+ indicates a gain of energy by the leaf; - a loss)

Humidity effects

As could be expected from a leaf action model based largely on a consideration of gas exchange, the humidity of the air, expressed as the water vapor density, is an important parameter. This point is illustrated in Figure 9, which shows transpiration as a function of air humidity at different levels of stomatal sensitivity. The feedback loop #4 (see Figure 3) dominates this set of relations, in that in a sensitive leaf the increase in transpiration that is expected from a drier environment is largely suppressed by stomatal closure. In a non-sensitive leaf (SENS = 0.1) the energy flux of transpiration rises to almost 500 w/m^2 or 0.71 ly/min. In a field array of such leaves an equivalent evaporation rate could well be 1.5 mm/hr, assuming a per unit land area loss twice that per unit leaf area (1 ly/min equals 1 mm/hr). In the irrigated desert in summer such rates have indeed been measured (Van Bavel, et. al., 1963). Figure 9 illustrates the water conserving role of a sensitive stomatal mechanism, while taking into account all the secondary effects upon leaf temperature, energy balance and photosynthesis.

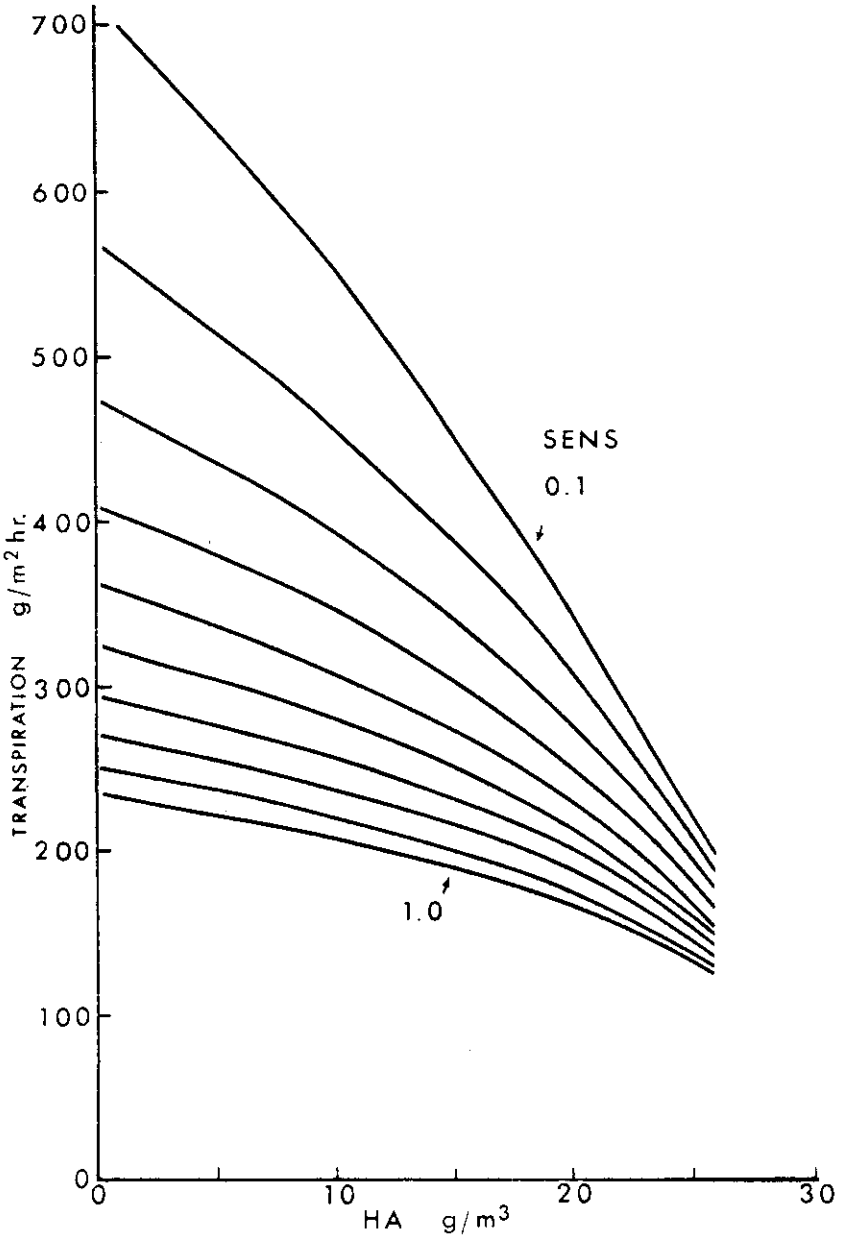

Figure 9. Calculated relation between transpiration in g/m^2 hr and air humidity in g/m^3 for different values of stomatal sensitivity to leaf water potential. All other conditions as in Tables 1 and 2.

Air humidity also plays a significant role in regard to photosynthesis, modulated somewhat by stomatal sensitivity, as shown in Figure 10. Here we predict that net carbon assimilation will be significantly enhanced by increasing air humidity, more so in the leaf type that is sensitive to water stress. Putting the results of Figure 9 and 10 together, we expect a very strong effect of air humidity upon water use efficiency. We define water use efficiency here conveniently as the mass ratio of CO_2 flux to H_2 flux, or NP/(1.47*LE) in the units employed here. The mass flux ratio is shown in Figure 11 and it is evident that from a humidity range from about 5 to 25 g/m^3 a six-to-sevenfold increase in efficiency is predicted. Curiously, the influence of stomatal sensitivity is about canceled. This type of finding is impossible to obtain by intuition or verbalization, and, thus, it shows one of the values of modeling.

Ambient carbon dioxide effects

In most leaf and plant modeling efforts the assumption is made that under normal field conditions ambient CO_2 levels will not deviate significantly from those in the bulk atmosphere and, therefore, this parameter is not included as a variable. (An exception is the study by Lommen, et. al. (1970), cited earlier, which simulates photosynthesis up to an ambient level of 5 g/m^3 CO_2). However, it is technically feasible to modify the CO_2 level in enclosures (Wittwer and Robb, 1964) and in the open field (Harper, 1970). Thus, there is reason to inquire about the potential of CO_2 level management. Figure 12 presents a simulation of net photosynthesis as affected by CO_2 level and compensation point, demonstrating the large effect of both, though above 2 g/m^3 (1200 ppm) CO_2 saturation develops. Figure 13

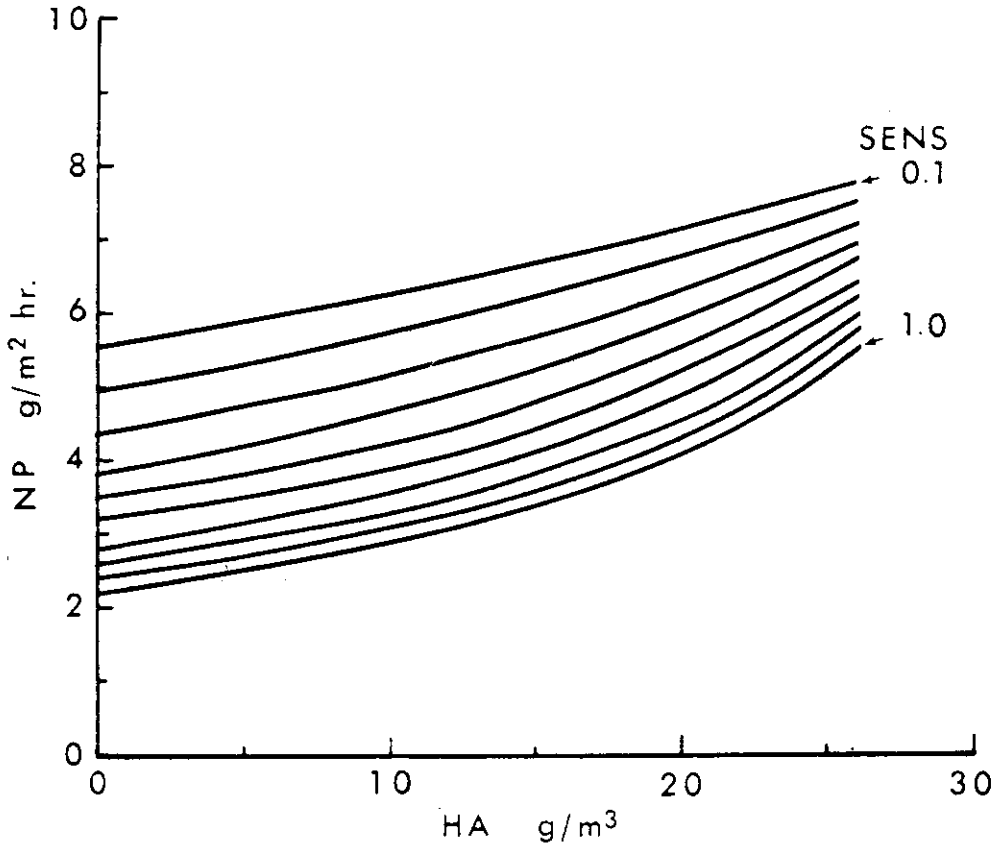

Figure 10. Calculated relation between net carbon dioxide exchange in g/m^2 hr and air humidity in g/m^3 for different values of stomatal sensitivity to leaf water potential. All other conditions as in Table 1 and 2.

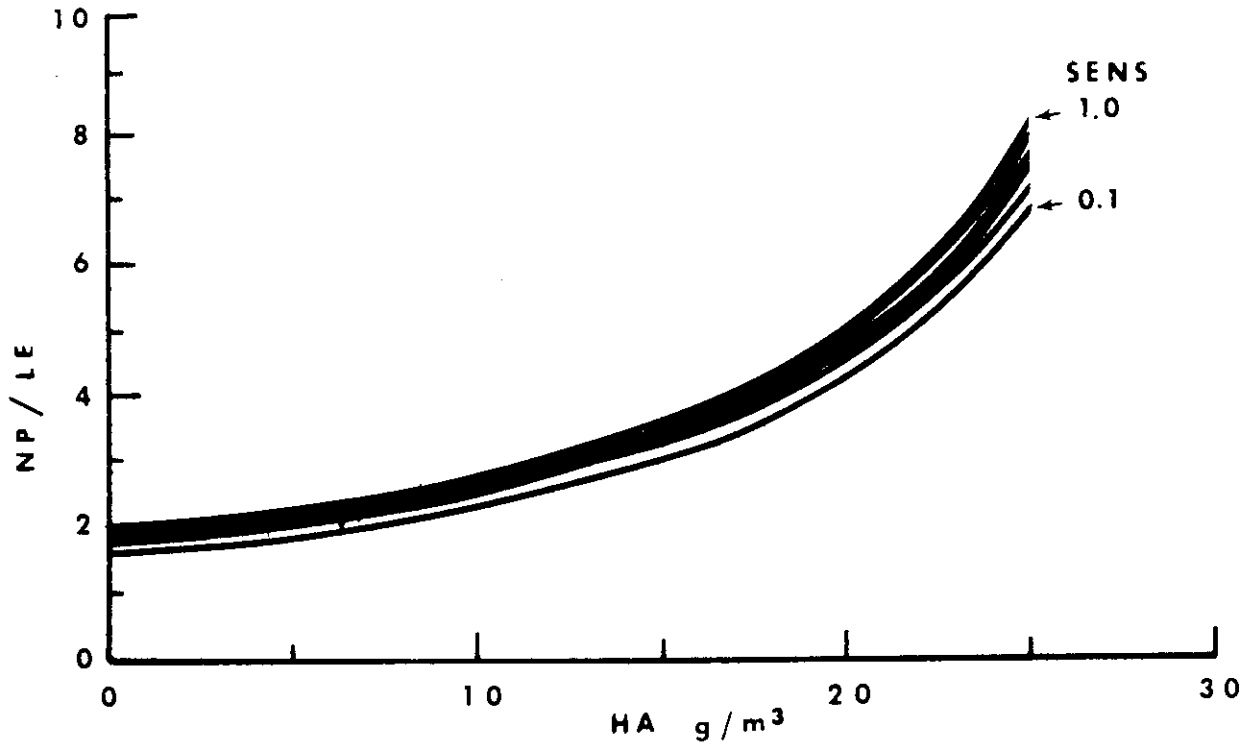

Figure 11. Calculated relation between water use efficiency (mass flux ratio) and air humidity in g/m^3 for different values of stomatal sensitivity to leaf water potential. All other conditions as in Tables 1 and 2.

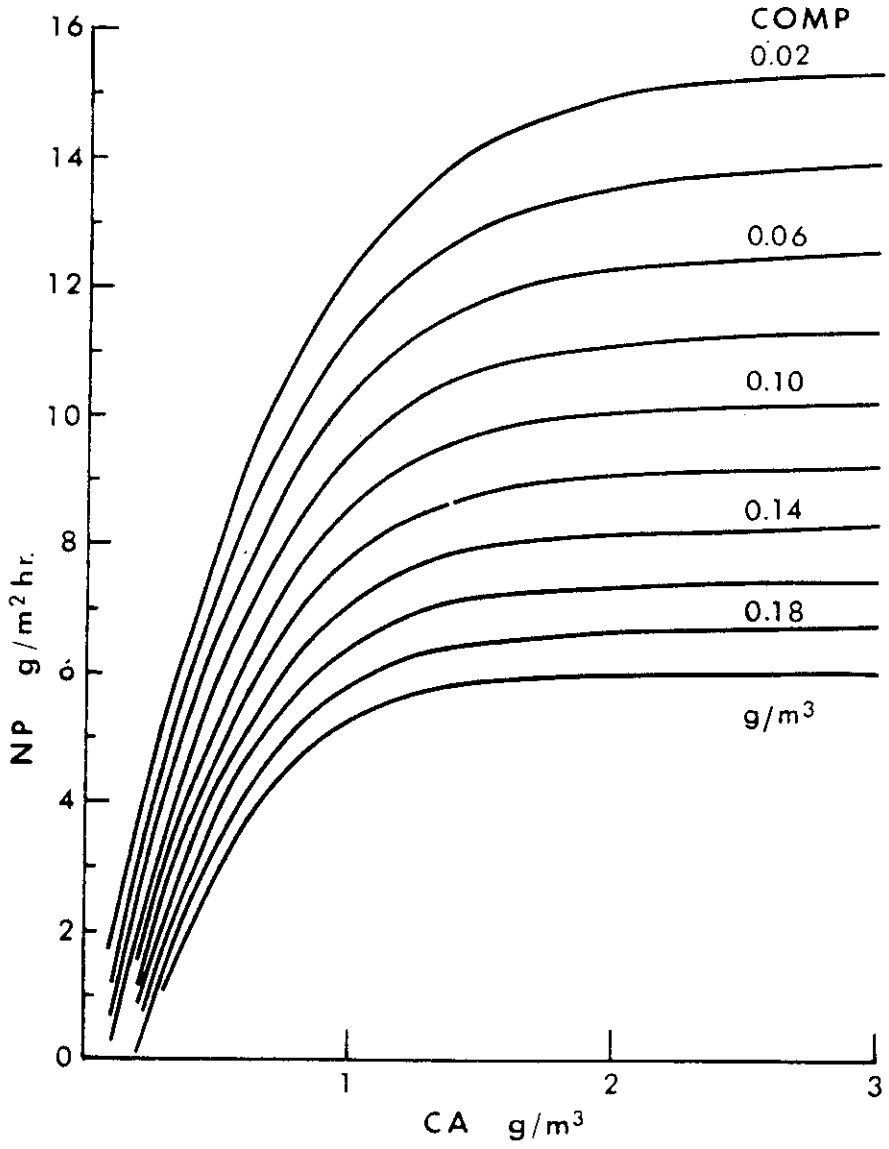

Figure 12. Calculated relation between net carbon dioxide exchange in g/m^2 hr and ambient CO_2 level in g/m^3 for different values of the CO_2 compensation point, also in g/m^3. All other conditions as in Tables 1 and 2.

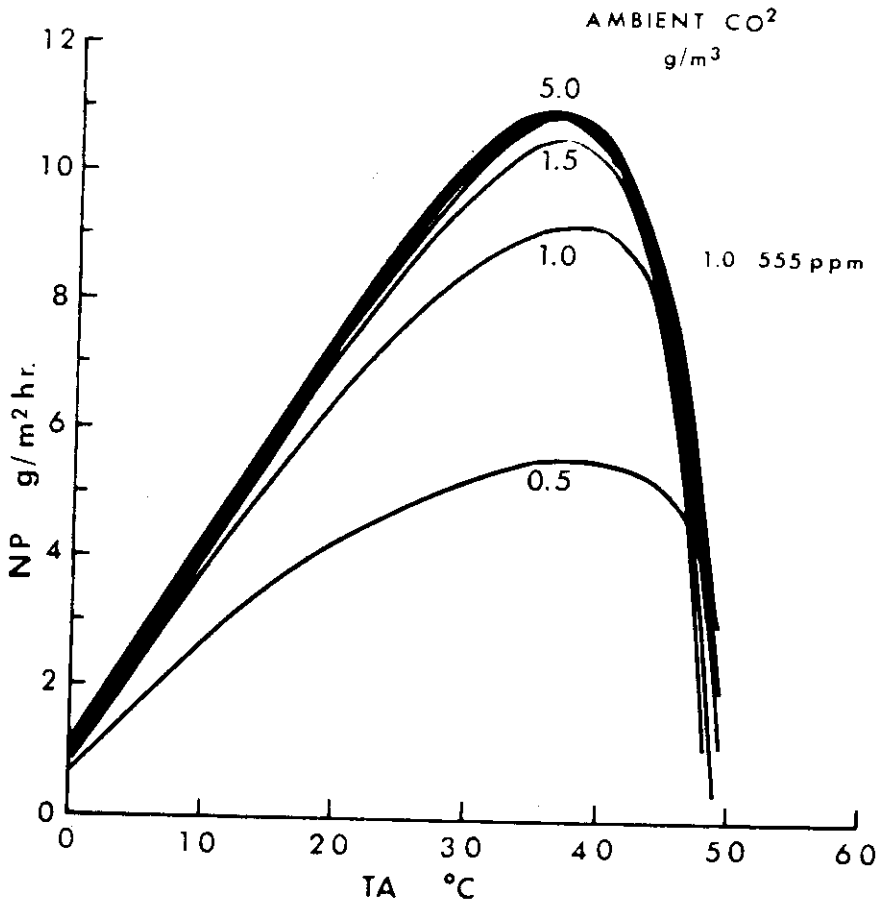

Figure 13. Calculated relation between net carbon dioxide exchange in g/m^2 hr and ambient temperature for different values of the ambient CO_2 level in g/m^3. All other conditions as in Tables 1 and 2.

shows the effect of air temperature at various levels of ambient CO_2. It shows a strong interaction between CO_2 level and air temperature.

When the effect of temperature upon transpiration is explored, as in Figure 14, we notice a strong, but opposite effect upon water loss, primarily because stomata close partially as the CO_2 level increases. Thus, we expect a compounded effect of the CO_2 level upon the mass flux ratio, or the water use efficiency. This effect is clearly shown in Figure 15, and it implies that CO_2 is the ideal antitranspirant, as it increases the mass flux ratio over a wide range of ambient temperatures.

Joint action of humidity and carbon dioxide level.

It has already been shown that increasing ambient humidity and carbon dioxide have analogous effects upon both transpiration and carbon dioxide assimilation. Thus, we can expect an additive effect, particularly on the ratio of assimilation to transpiration. This is clearly observed in Figure 16, which is an expansion of Figure 11. This calculation shows that very high water use efficiencies, up to 15%, may be anticipated by combining high concentrations of water vapor and CO_2 in the leaf environment. Commonly observed figures for field crops are in the 1-2% range.

Light and radiation effects.

In simulating the effect of variations in light level, one must take into account that the total radiant must be changed also, as it does in nature. Changes in light level affect not only photosynthesis but also the energy balance of the leaf. Thus, the effect of an increase in light may be partially offset by stomatal closure, due to the increased transpiration. There are secondary effects of

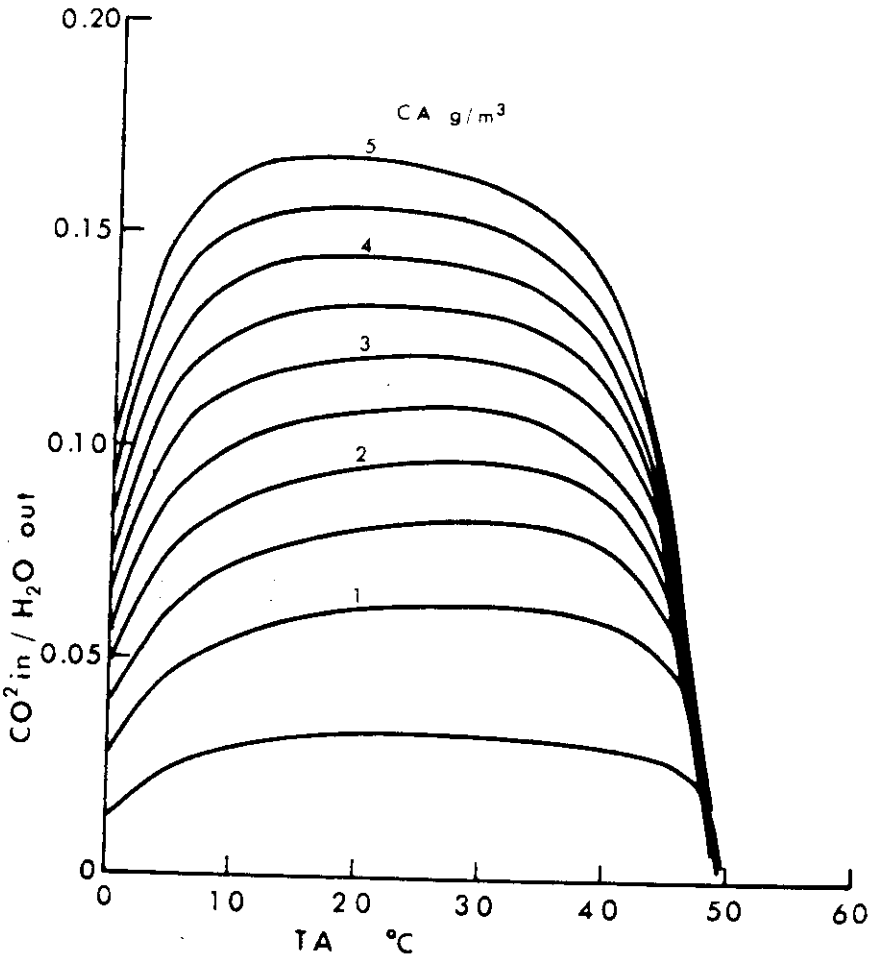

Figure 15. Calculated relation between water use efficiency (mass flux ratio) and ambient temperature for different values of the ambient CO_2 level in g/m^3. All other conditions as in Tables 1 and 2.

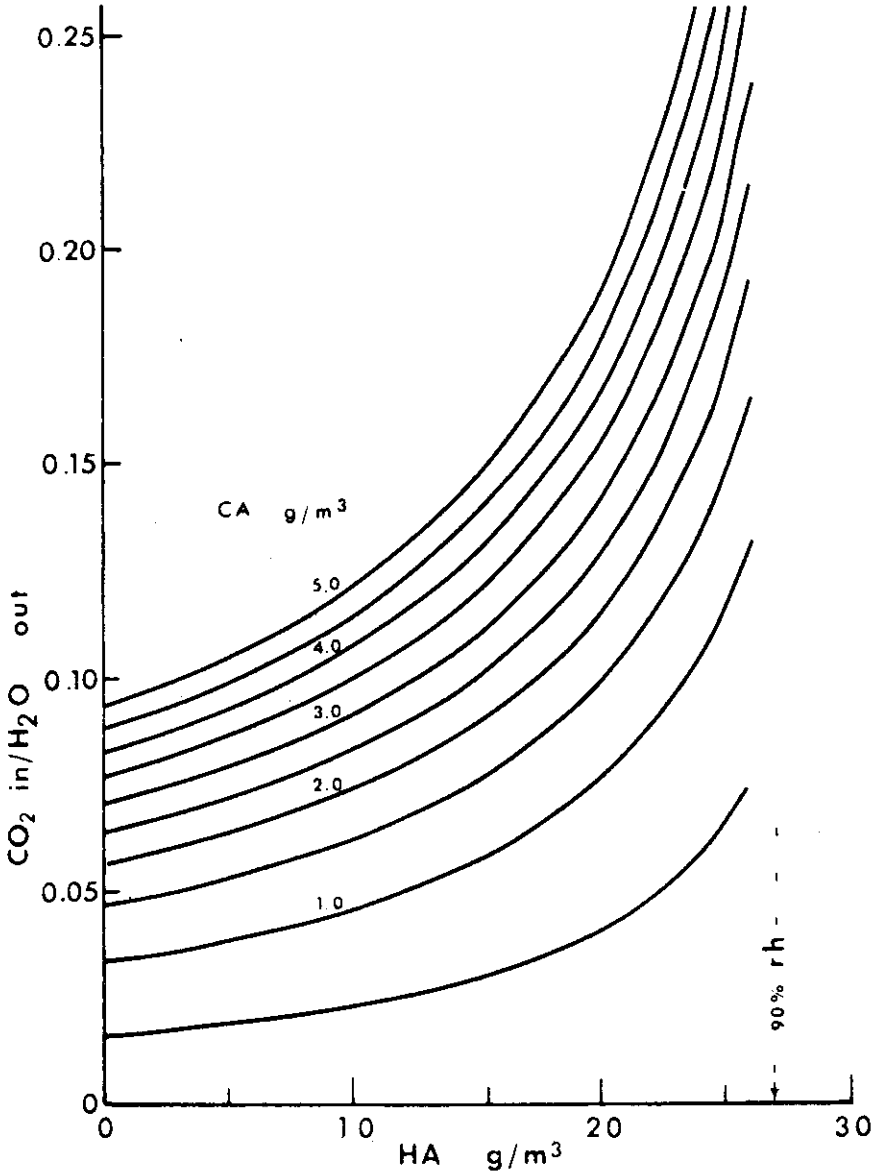

Figure 16. Calculated relation between water use efficiency (mass flux ratio) and ambient humidity in g/m^3 for different values of ambient CO_2 level in g/m^3. All other conditions as in Tables 1 and 2.

leaf temperature to be considered as well. An example of these complexities is given in Figure 17, which suggests that the light "saturation" value for NP could be much lower in leaves with sensitive stomata, than in those that can keep them open in spite of water deficiencies.

Another illustration is given in Figure 18, which suggests that plants may have an essentially flat response above 120 W/m^2 of PR regarding water use efficiency. The significance of the compensation point is also obvious.

DISCUSSION

A simulation is only a calculation of what would happen if certain presumptions were true, or sufficiently accurate. It warns us, however, not to ask certain overly simple questions (nor to believe certain answers), such as: what is the effect of air temperature upon transpiration? Even in the case of a well-formulated question, the answer may at best be a table, or a set of curves, and specific plant properties, often resulting from adaptation to a given environment, will determine the specific modeling results.

Certain generalities may, nevertheless, be stated as a cautious extract of the manipulation of our model. The principal environmental factors that determine leaf gas exchange are the ambient gas concentrations, and, next to these, the light and radiation load. Air temperature and air speed, in particular, are found as less critical factors.

Of the relevant plant parameters, an unexpectedly strong role is played by the CO_2 compensation point and, also, by stomatal sensitivity to water stress. Leaf dimension and stomatal numbers are not as critical, and breeders or agronomists may take some guidance

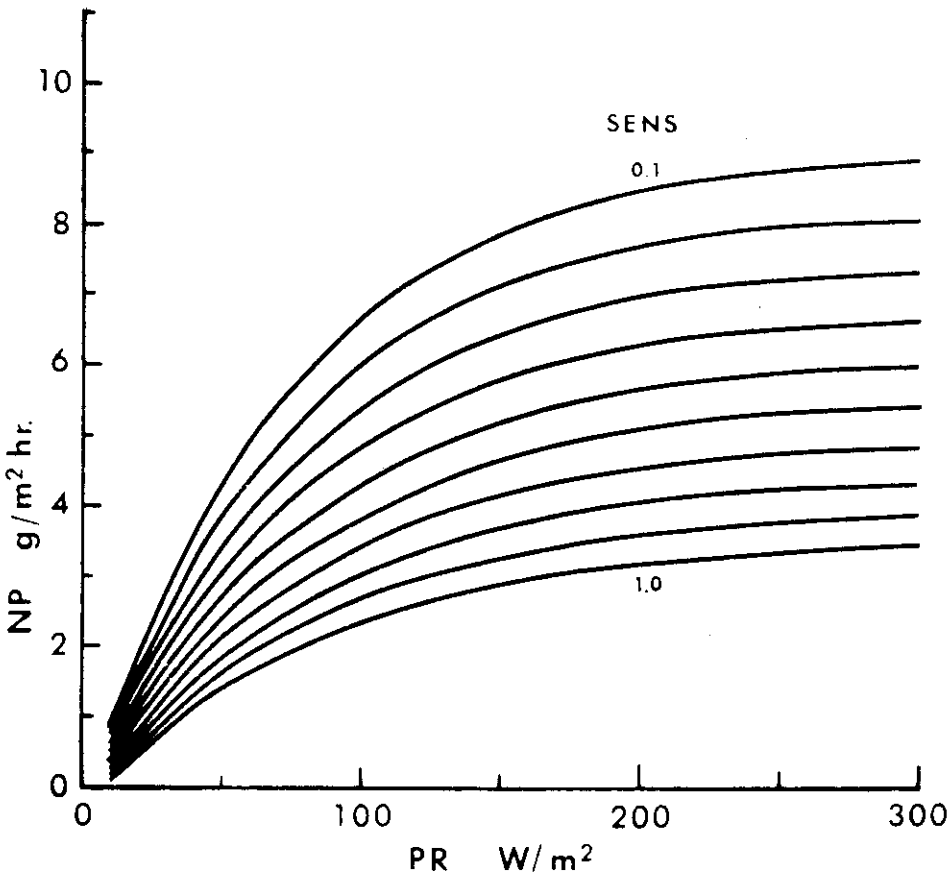

Figure 17. Calculated relation between net carbon dioxide exchange in g/m^2 hr and light level in W/m^2 PAR for different values of stomatal sensitivity to water potential in steps of 0.1. All other conditions as in Tables 1 and 2.

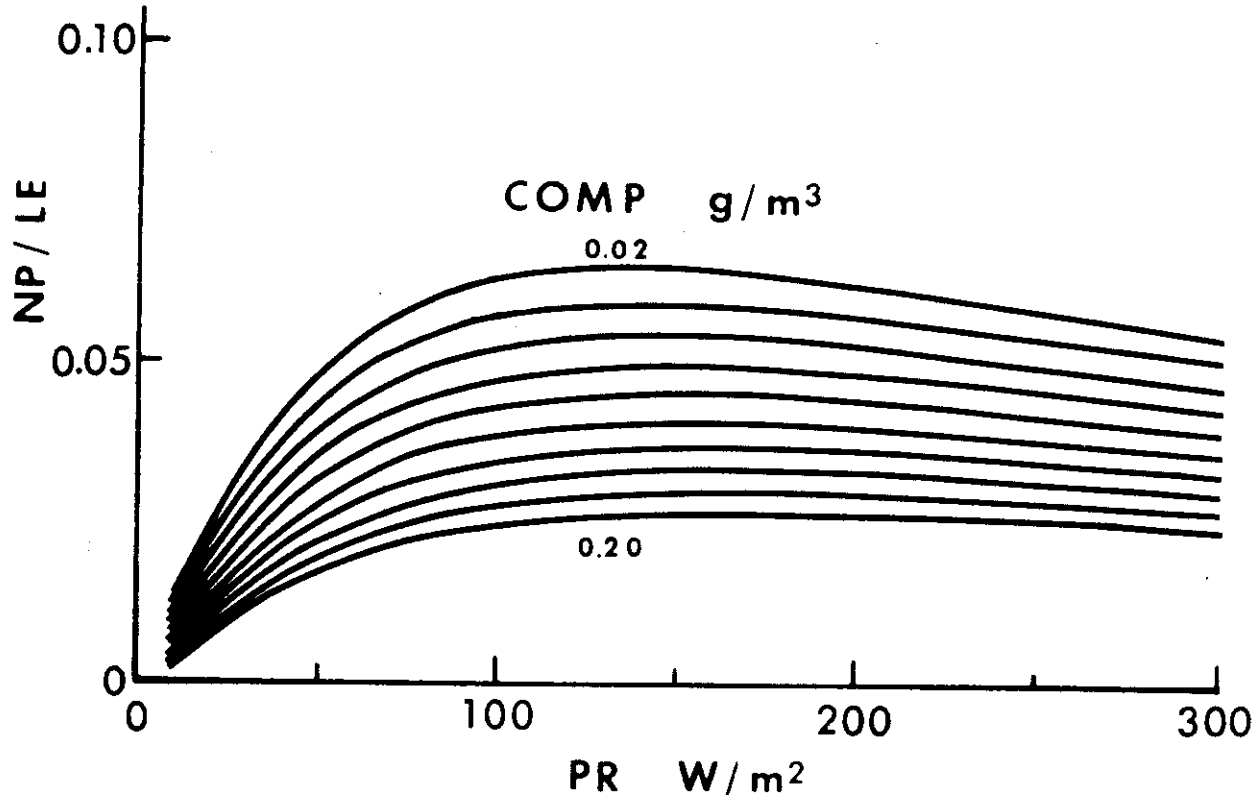

Figure 18. Calculated relation between water use efficiency (mass flux ratio) and light level in W/m^2 PAR for different values of the compensation point in g/m^3. All other conditions as in Tables 1 and 2.

from these suggestions. Stomatal sensitivity is known to vary widely among crop plants, but quantitative data are scarce. These analyses may stimulate studies paralleling those made by Kanemasu and Tanner (1969). Varietal differences in compensation point (Moss, 1969) are already being explored by geneticists, and perhaps this new aspect of crop improvement techniques can be usefully expanded, by its incorporation into models of plant growth and yield.

Part of the stimulus of a modeling effort is to suggest new experiments to verify the predictions made and to measure the data that are required for model application. A clear need is indicated by this work to measure the critical aspects of stomatal behavior in important crop species: effects of temperature, of internal CO_2 level, and of water stress, the last one being of immediate practical impact as it relates to plant performance under conditions of limited water availability.

The present work has obvious limitations. It can be improved by considering the plant as a dynamic and transient organism in which water and CO_2 are subject to storage and release. The dynamics of soil water depletion and of the diurnal cycle of the environment should be added to the picture. More fundamental models for the photosynthetic action must be incorporated and, above all, an improved model of stomatal operation is needed for further progress.

ADDENDUM I

The relation (10) is obtained as follows. Of the incident horizontal shortwave radiation SR (as measured with a standard pyranometer) one-half is taken to be in the photosynthetically active waveband and to be entirely absorbed by the leaf. In contrast, it is assumed that 30% of the remaining half is absorbed. Thus, the shortwave term of TR equals 1.3 PR. The value of incoming longwave sky radiation, assuming a clear sky, is taken as 250 W/m^2 (blackbody temperature of -16 °C), whereas the outgoing earth radiation is estimated at 450 W/m^2 (blackbody temperature of 25 °C). As this radiation is fully absorbed by the leaf, we obtain as a first approximation

$$TR = 700 + 1.3\ PR \quad W/m^2$$

For particular conditions this approach is too simplistic. For outdoor conditions and application to a developed crop canopy it is more practical to express PR and TR in terms of SR, which is commonly measured. A closer estimate of PR than given above is:

$$PR = 0.47\ SR$$

and for estimating TR, we use the well-known Brunt formulation for the incoming long wave radiation (LR)

$$LR = \sigma(TA)^4\ (0.605 + 0.039\ \sqrt{1.41\ (HA)}) \quad W/m^2$$

TA being the air temperature in K and HA the humidity in g/m^3.

The outgoing earth radiation (ER) is estimated as

$$ER = \sigma(TA)^4 \quad W/m^2$$

and the shortwave absorbed component as

$$(0.47 + 0.3 \times 0.53)\ SR = 0.63\ SR$$

implying an approximate albedo of 18%, and an equal fraction of the shortwave radiation to reach the ground surface. Thus the total

expression becomes:

$$TR = \sigma (TA)^4 \left(1.605 + 0.039 \sqrt{1.41\ (HA)}\right) + 0.63\ SR$$

Although this approximation is still somewhat arbitrary, it is certainly workable and has given us good results in the estimation of leaf temperatures in work not reported here.

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GLOSSARY

Abbreviation	Definition	Unit
CA	carbon dioxide density in air	g/m^3
CL	carbon dioxide density in leaf	g/m^3
COMP	CO_2 compensation point	g/m^3
DRESP	dark respiration rate	$g/hr\ m^2$
ERFC	complementary error function	none
FCNT	temperature response function	none
HA	(absolute) air humidity	g/m^3
HL	(absolute) leaf humidity	g/m^3
K1, K2, K3	constants	
LE	leaf transpiration rate	W/m^2
LH	latent heat of vaporization of water	J/g
LL	leaf dimension	m
LR	long-wave (thermal) radiance of leaf	W/m^2
NP	net carbon exchange (photosynthesis)	g/m^2 hr
NPMAX	maximum gross photosynthesis	g/m^2 hr
PR	photosynthetically active irradiance	W/m^2
RA	boundary layer resistance	s/m
RL	leaf diffusion resistance	s/m
RLL	leaf diffusion resistance, lower	s/m
RLMAX	maximum leaf resistance	s/m
RLMIN	minimum leaf resistance	s/m
RLU	leaf diffusion resistance, upper	s/m
RTOT	total leaf resistance, water vapor	s/m
RTOTC	total leaf resistance, carbon dioxide	s/m
SA	air speed	m/s

Abbreviation	Definition	Unit
SE	sensible heat exchange	w/m^2
SENS	stomatal sensitivity to water potential	1/bar
SH	specific volumetric heat capacity of air	$J/deg\ m^3$
SRPL	specific resistance of plant	$bar\ s/m^2/g$
TL	leaf temperature	°C
TLMIN	reference temperature for stomatal opening	deg C
TR	total radiant load of leaf	W/m^2
WPOT	leaf water potential	bar

9. APPENDIX 2

TOWARDS REALISTIC SIMULATION OF THE NATURAL PLANT CLIMATE

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(Presented at the UNESCO Symposium on "Plant Response To Climatic Factors," Uppsala, 15-20 September, 1970)

Abstract

Controlled environments that simulate outdoor conditions realistically are indispensable tools in developing accurate predictive methods for plant behavior. Currently, the state of the art is deficient, notably in regard to providing sufficiently high light levels, simulating natural air flow, regulating the carbon dioxide level, and correctly specifying and controlling ambient humidity. It is proposed that in regard to all four points, generally available commercial components for lighting, gas analysis and air conditioning can be used in a simple fashion to achieve rational goals with respect to range, control accuracy, and response speed. Performance data are cited for a pilot model constructed according to the principles given.

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TOWARDS REALISTIC SIMULATION OF THE NATURAL PLANT CLIMATE

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Introduction

Our aim is to understand the effects of natural variation in environmental factors and to predict plant response under outdoor conditions. Nevertheless, we will find ourselves compelled to conduct studies that are controlled with regard to the entire environment, in order to, (1) establish effects of single parameters and, (2) verify models that predict multifactor effects.

As Gaastra (1969), for example, has noted earlier, it is not necessary to duplicate the magnitude and the variation of the environmental factors as found outside. But it is very necessary to elicit vital responses from the plants comparable to those occurring in nature, for example, transpiration rates, photosynthesis and respiration rates, leaf expansion rates, development rates, stomatal action, root proliferation and activity, and so on. Also, though single leaf and single plant studies will always be important, the essential data will have to be obtained from plant communities in which the characteristic self-shading, humidity build-up, carbon dioxide depletion and canopy temperature distribution can be simulated. Finally, and with special reference to agricultural crops, it is necessary that plants can be

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grown to maturity so that yield data may be obtained.

Without intent to criticize any specific installation, we may safely state that all known growth chambers or phytotrons suffer from some or all of the following deficiencies with regard to the general criteria given above.

1. Light levels are too low, compared to natural conditions, seldom exceeding 150 w/m^2 PAR (=0.4 - 0.7 micron waveband) A sharp fall of radiance with distance from the lights is common.

2. Total radiant energy load is usually even lower, by comparison, seldom in excess of 200 w/m^2.

3. Air speed is usually small, less than 0.2 m/s, and random.

4. Measurement and control of CO_2 is absent.

5. Dimensions are insufficient to allow small stands of plants to grow to maturity.

6. Responsiveness of the systems for control of air temperature and humidity is often poor, because the time constants of the sensors of the control mechanisms, and of the heat sinks and sources are much too large, of the order of several minutes.

What are realistic goals and methods in plant climate simulation and control?

From a design point of view a logic sequence of goals can be noted in the diagram shown in Figure 1. The selection of a goal regarding lighting is an independent input and ought to preceed all other options. The next independent choices are those of the dew point range and air speed. All following specifications must take the previous two into account. In the following we discuss goals and techniques for each major parameter to be simulated.

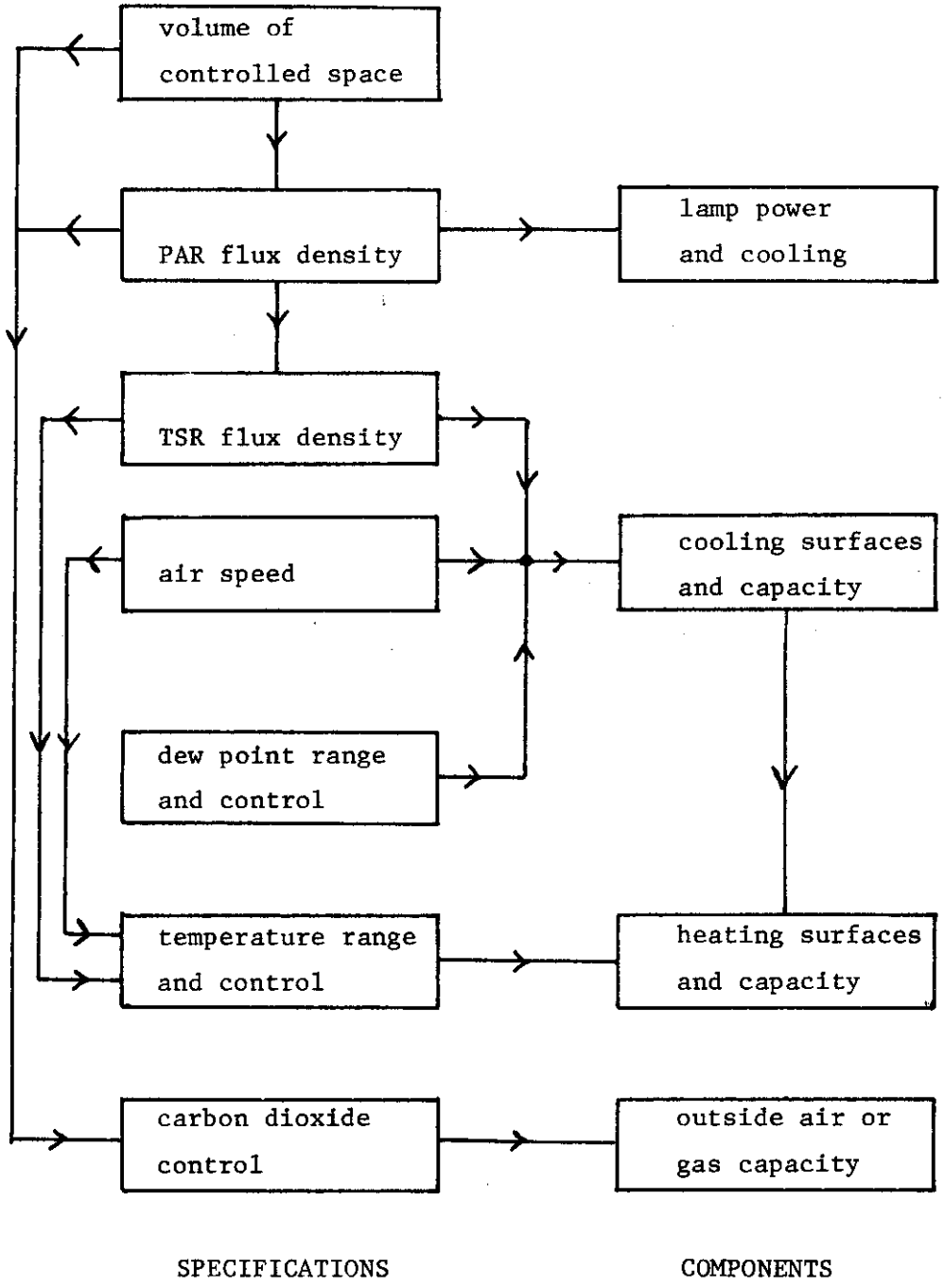


Figure 1. Flow chart of objectives and ensuing technical specifications in environmental simulation design. PAR = photosynthetically active radiance; TSR = total shortwave radiance.

a. Illumination and irradiance

The goal here is to maintain radiant flux density levels at the leaves that result in rates of photosynthesis and leaf temperatures comparable to the natural environment. Because of the "light saturation" effect, well known for individual leaves, it has been assumed that "saturation" light levels would suffice for simulation. This is false, because of the generally non-normal orientation of leaves and, more so, because of mutual shading in stands. The photosynthetically active irradiance by natural light can be as high as 500 w/m^2 (0.7 $cal/cm^2 min$) without "saturating" a fully developed canopy, as recently shown for soybeans by Egli et al. (1970). The corresponding total short wave radiation (less than 2 microns) is about twice the PAR.

Fluorescent lamps can provide only about 1/4 of the maximum natural PAR. Arc lamps have a much greater output, are smaller, and allow denser packing. Also, they have more realistic ratios of PAR to TSR (total shortwave radiation). In Table 1, the characteristics of four common lamp types are given when used in a luminous ceiling of an artificial plant environment.

Table 1 suggests that, using lamp types now commercially available, realistic PAR levels can be obtained. For the arc-type lamps, reflectors are available that direct light downward with efficiencies of 70% or more. The advantage of doing so is apparent from the data for metal halide lamps. Not only is the PAR level 3.3 times greater than that for fluorescent lamps, but the cooling requirement for the removal of excess heat in the lamp compartment is not much greater.

The data of Table 1 are illustrative only and will vary with

Table 1. Typical PAR and TSR flux densities obtainable with four different lamp types, derived from actual installations or designs.

Type	Commercial Type **	Lamp Density kw/m^2	Irradiance PAR* w/m^2	Irradiance TSR* w/m^2	(Illuminance) (klux)	Cooling kw/m^2
Fluorescent	CW/VHO 215 w	1.6	130	150	(32)	1.4
High Pressure Mercury	HPL-33 400 w	5.8	400	840	(127)	5.0
High Pressure Sodium	Lucalox 400 w	3.6	450	900	(167)	2.7
Metal Halide	Metalarc (in reflector) 400 w	2.4	425	850	(137)	1.6

* Below a barrier of 0.9 transmittance in the 0.4 - 2.0 micron waveband.

** Brand names of commercial lamps are given as representative examples, not to indicate preference.

individual brands and the age of the lamps. With the sodium vapor and metal halide lamps, greater lamp densities can be achieved than shown.

Since with even the most efficient lamps more than 65% of the lamp power is turned into sensible heat, it is mandatory that a light barrier made from glass or clear plastic be used. In some lamps this may also be desirable to exclude ultraviolet radiation (less than 0.3 micron wave length). Airtight sealing of the plant chamber will also be easier with a transparent ceiling.

b. Air circulation

Gaastra (1969) has earlier made a plea for greater air speeds in climate rooms. His argument is that in the usual becalmed environment transpiration rates are likely to be erratic and abnormally low, because of the high resistance of the leaf boundary layer. To this we can add that the semi-closed conditions of stomata at light levels below 150 w/m^2 PAR (see Ehrler and Van Bavel, 1968) aggravates the problem even further in the conventional artificial environment.

In order to achieve boundary layer resistances of less than .25 s/cm, - a value suggested by the calculations of Gaastra - a leaf of dimension 4 x 4 cm must be ventilated on its edge by air with a velocity of about 0.5 m/s (1.8 km/h). This simple calculation (see Monteith, 1964) suggests that realistic simulation requires unidirectional, horizontal air flow of 1 m/s and more. To achieve high rates of transpiration and associated depressions of leaf water potential and leaf water content, air speeds up to 5 m/s (18 km/h) may be desirable. The model calculations of Gaastra (1969), Gates (1968), and others demonstrate also that, at low air speeds and high radiation levels, unrealistic differences between air and leaf temperature result and it

is likely that the leaf temperatures will vary greatly among themselves under such conditions.

In order to simulate natural conditions, air flow must be horizontal. In dense plant arrangements in a chamber this will result in the typical stagnation of the air in the canopy that is found outside. It would seem impossible to simulate natural wind profiles with simple means, but so far there is no known reason for wanting to do so.

For experimental purposes it is further desirable, that the airspeed is variable and can be as high as 5 m/s, as noted above. This may interfere with the efficient and constant operation of the cooling coils, in that high air speeds increase the sensible heat ratio, whereas the principal purpose of the coil is to extract latent heat. We propose here a novel approach, which will be used in a chamber with a floor area of 5 m^2, now under construction at Texas A&M University. In it the air circulation through the cooling coil and through the system as a whole are independently variable. This VARES (variable air ratio environmental simulation) principle is illustrated in Figure 2. A computer program to give the optimum air speed ratio for a given set or range of conditions is under development.

c. Humidity and temperature control

Control of air humidity has probably been the least satisfactory and most frustrating aspect of climate simulation. The problems are due to (1) unjustified preference for specifying the conditions in terms of relative humidity, rather than of absolute humidity or dewpoint, (2) attempts to control humidity with a wet bulb device, (3) lack of appreciation for the technical problem of controlling the dewpoint below 0°C and (4) imposition of unwarranted requirements as

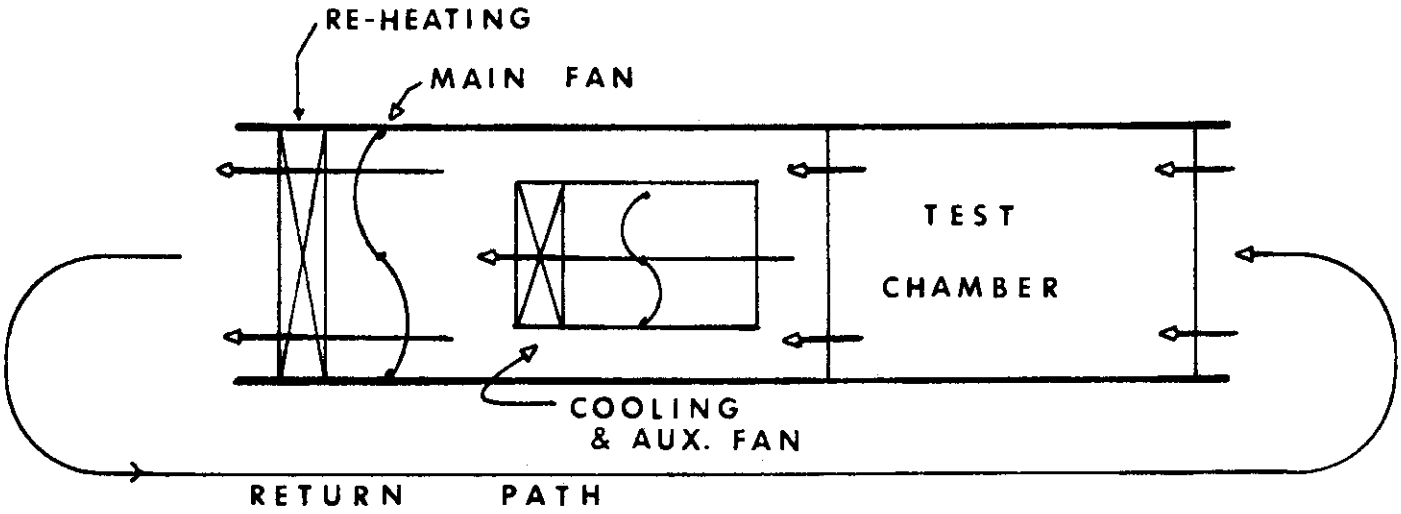


Figure 2. Schematic arrangement of VARES (variable air ratio environment simulator). The speed of the two fans can be independently varied.

to accuracy of control upon chamber designers and suppliers.

Humidity control in the plant environment has as its purpose the regulation of transpiration, or, more generally, the state of hydration of plant parts and tissues. This, in turn, is determined directly by the absolute humidity - more commonly measured as vapor pressure or, as a dew point value. This factor, then, must be controlled and the system capability must be expressed in the attainable range and control accuracy of vapor pressure or dew point.

During the growing season of many crop plants the absolute humidity changes are not profound, representing mostly alternating masses of polar and tropical, or continental and marine air. During the period March - November the mean dewpoint in the U.S. at screen level varies from -3°C to 20°C, exclusive of higher elevations. Even in the low deserts of Arizona and California, June dewpoints are around 5°C.

Thus, we propose that for many purposes dewpoint control from 1 to 20°C shall suffice, simplifying the designing task greatly by avoiding values below freezing. In order to assess the required accuracy, it should be remembered that the energy balance principle that governs water use by vegetation outside, is equally applicable in a growth chamber. The combination formula as given by Penman and others (see Van Bavel, 1966) suggests that control of evaporation by leaves to 5% of its absolute value, requires typically no more than a 25% control of the absolute humidity. Even at a dewpoint of 1°C a control accuracy of 1°C, therefore, is quite acceptable, and easily manageable. This proposition is illustrated in Table 2 in which we calculate the increase in evaporation that results from a 1°C decrease in dewpoint in 4 selected environmental situations.

Table 2. Increase in evaporation rate from a well-watered canopy resulting from a dew point decrease of 1°C. The conditions are given as the radiant balance of the surface, the ambient air temperature and air speed, and the dew point. Calculations are based on a drag coefficient of 0.006.

Conditions		Evaporation rate per m^2	Increase
700 w/m^2 5 °C 5 m/s DP 3 °C	"cold desert"	0.533 kg/h	3%
700 w/m^2 35 °C 5 m/s DP 10 °C	"hot desert"	1.445 kg/h	1%
700 w/m^2 30 °C 1 m/s DP 20 °C	"tropics"	0.866 kg/h	< 1%
400 w/m^2 20 °C 5 m/s DP 15 °C	"temperate"	0.554 kg/h	5%

Having made the point that dewpoint or absolute humidity control is rational and not demanding in range nor accuracy, as long as it can be above 0°C, the remaining question is how to best accomplish it.

Since the wet bulb temperature is an ambiguous indication of humidity, it makes a poor control element. A dewcel, so-called, (see Tanner and Suomi, 1956, for example) can be used. In our experience a much simpler approach is to control the temperature of the condensing element in the air conditioning apparatus. The fact that plants lose water continually in large amounts makes this possible and this option has been overlooked by designers of plant chambers.

With a well-designed coil for cooling and dehumidification the temperature of the air leaving the coil is very close to the dewpoint. Thus a thermometer of any desirable nature (thermocouple, resistance wire, thermistor, diode, or liquid expansion) can be used to set the dewpoint by regulating the flow of coolant through the coil.

In our experience, dewpoint control of 0.2°C is not at all difficult, provided the control system has the requisite sensitivity and response time. Both items are featured by standard industrial control elements.

Air temperature control, as long as it is separated entirely from humidity control, is straightforward and consists of controllable reheat of the air after it leaves the dehumidification element. Air temperature control to the nearest 0.5° C or better should not present any problem with standard industrial components.

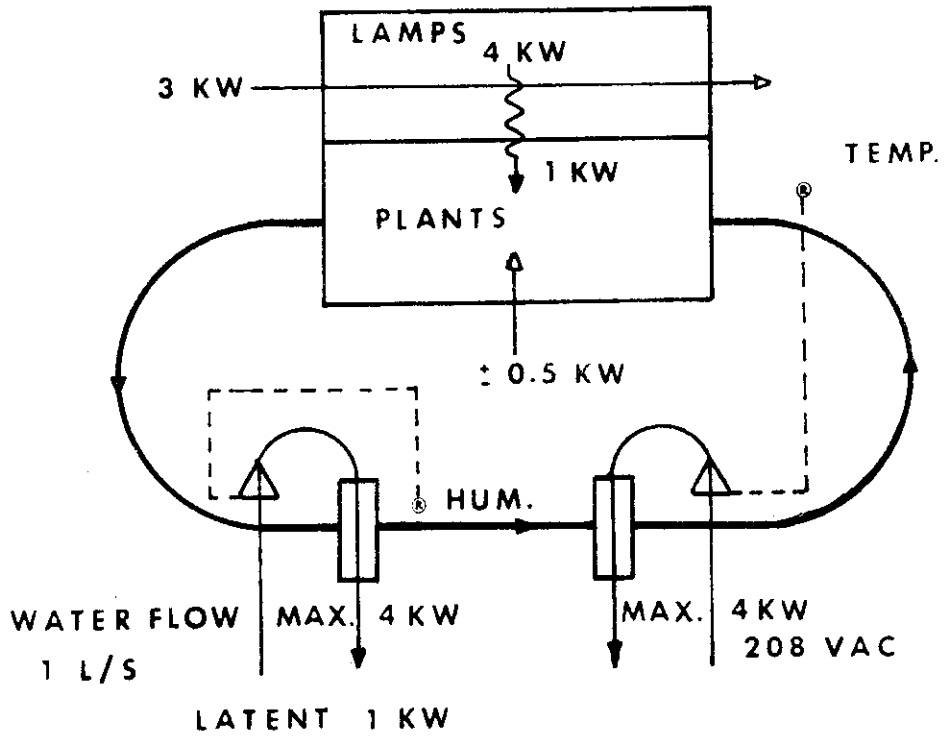
In sum, a rational approach to adequate control of humidity and temperature can be based upon the recognition of one's true objectives and the fact that plants impose a relatively large latent heat load upon the system. Proper insulation will tend to make this latent-to-

sensible heat load ratio even higher. Thus the appropriate method is to lower the air temperature to the desired dewpoint and to reheat it to the desired temperature. In Figure 3 we give data that illustrate the capabilities of an existing climate chamber based on the principles discussed here. Superficially, such a system is wasteful of energy and, often, engineers and suppliers try to overcome this by cycling or alternating heating and cooling. In terms of performance these economies are false.

d. Carbon dioxide concentration

In first analysis, plants andpplant stands tend to respond linearly to ambient CO_2 levels (see e.g. Baker, 1965 and Egli et al., 1970). One would think that the recording and control of such a variable would be a standard feature of plant environments, but this is not the case. Usually a certain amount of "fresh" air is led into the plant space, and it is assumed that this will do. In the first place, the "fresh" air may be quite variable in CO_2 content, particularly if large buildings or parking lots are near to the intake. Variation between 300 and 350 ppm are common. The air inside buildings is even more subject to variation.

We submit that a serious study of the effect of environment upon plant function must provide a record of the CO_2 level. Once this is done, control can be provided with little additional effort. For continuous operation, a compensation technique as suggested, for example by Koller and Samish (1964), is suitable also for large chambers. CO_2 gas in either pure or diluted form is admitted to the chamber so as to keep the level constant as measured by an infrared gas analyzer. During periods of darkness the CO_2 level will build up to where the evolution rate equals the leakage rate of the chamber.



total volume	:	3.7 m^3
plant chamber	:	.60 x .60 x 1.80 m = .65 m^3
air speed	:	1.2 m/s = .43 m^3/s
lighting	:	10 lucalox at 400 w = 3.6 kw/m^2
barrier	:	3 mm clear lucite
radiant load	:	1 kw, 420 w/m^2 PAR
cooling	:	chilled water coil + automatic mixing valve
heating	:	nichrome wire heater + SCR power controller
temperature	:	5° - 40° C $\pm$ 0.3° C
dewpoint	:	3° - 35° C $\pm$ 0.2° C, or (ambient - 10)° whichever is more
carbon dioxide	:	100 - 2000 ppm
response time	:	about 0.1° C per second

Figure 3 Performance characteristics of a 1 m^2 pilot model environmental simulator for plant production experiments. Dotted line shows control connection to valves.

Since respiration is not considered sensitive to CO_2 level, this appears to be without objection.

For the system described in Figure 3, a typical CO_2 fixation rate is 25 cm^3/min, or 7 ppm CO_2/min. Such a change is easily detectable and can be counteracted by an intermittant CO_2 flow rate of 100 cm^3/min, for example. To achieve a minimum depression of 10 ppm by means of "fresh" air introduction, one would require 2.5 m^3/min, almost an entire air change every minute and 10% of the entire circulation. The problem thus raised for temperature and humidity control is obvious.

In terms of control accuracy, absolute infrared gas analyzers can be calibrated in the 300 ppm range with an accuracy of about 1 ppm (see Bate et al., 1969), and control action can be obtained with deviations from set point less than 3 ppm without undue complications. Such specifications are well in excess of requirements of the usual ecological experiments.

Summary

The usefulness of artificial environments for ecologically oriented research on plant behavior can be greatly improved over current practices by (1) increasing maximum irradiance to approximately 500 w/m^2 PAR and 1000 w/m^2 TSR, (2) controlling the level of ambient carbon dioxide, (3) increasing the air flow up to 5 m/s and making it horizontal and variable, (4) by controlling the absolute humidity.

We show that the above goals can be achieved by (1) using modern arc lamps, separated from the plant compartment by a transparent barrier, (2) designing the plant chamber as a closed, recirculating system with CO_2 injection, (3) separating the air flow over the conditioning surfaces from that through the plant chamber, making the latter

independently variable, and (4) by setting realistic goals for range and accuracy of control for the absolute humidity, rather than relative humidity, and achieving them by controlling the temperature of the condensing coil.

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C*************************************************************************
C 10.  APPENDIX 3
C
C         THIS PROGRAM IS REPORTED IN.........
C                   A MODEL OF GAS AND ENERGY EXCHANGE REGULATION
C                   ---------------------------------------------
C                        BY STOMATAL ACTION IN PLANT LEAVES
C                        ----------------------------------
C
C                                      BY
C
C                   C. H. M. VAN BAVEL, D. W. DEMICHELE AND J. AHMED
C
C         ALL ENQUIRIES CONCERNING THIS PROGRAM SHOULD BE DIRECTED TO...
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C                   427 BIOLOGICAL SCIENCES,
C                   TEXAS A&M UNIVERSITY,
C                   COLLEGE STATION, TEXAS 77843
C                   (713) 845 - 7110
C
C
C*************************************************************************
C
C         THE PURPOSE OF THE MAIN PROGRAM IS TO SUPPLY THE ENVIRONMENTAL
C         INPUT PARAMETERS TO THE SUBROUTINE BALANS AND PRINT THE
C         SIMULATION RESULTS BY CALLING THE SUBROUTINE OUTPUT
C
  3        COMMON / PARAM1 / CL, EB, ERFC, HL, LE, LH, LR, NP, PB, RA,
          1                  RL, RLL, RLS, RLU, RTOT, RTOTC, SE,
          2                  SH, SR, TL, TLC, WPOT, WPOTS, WPTMIN
  4        COMMON / PARAM2 / COMP, DRESP, FCNT, K1, K2, K3, LL, NPMAX,
          1                  RLMAX, RLMIN, SFNS, SRPL, TLMINC
  5        COMMON / PARAM3 / CA, ER, HA, HAIR, PR, SA, TA, TAC, TR, I
  6        HA = 18.1
  7        SA = 2.0
  8        TAC = 30.0
  9        CA = 0.575
 10        PR = 300.0
 11        TR = 700.0 + 1.3 * PR
 12        WPOTS = 0.0
 13        TA = TAC + 273.16
C
C            IF SIMULATION ON FIELD EXPERIMENTAL DATA IS DESIRED
C            TR SHOULD BETTER BE CALCULATED FROM BRUNT'S FORMULA AND AIR
C            HUMIDITY HA SHOULD BE CALCULATED FROM THE DEW POINT
C            TEMPERATURE ( DPTC IN DEGREE CENTIGRADE ). THUS TR AND HA
C            WILL BE CALCULATED BY INVOKING THE FOLLOWING THREE DEFINITION
C            CARDS WHICH HAVE BEEN PROVIDED AS COMMENT CARDS BELOW.
C      ER = C1 * TA ** 4
C      TR = ER * (1.605 + 0.039 * SQRT (1.41 * HA )) + 0.63 * SR
C      HA = 1323.5*EXP(17.2694*DPTC / (237.3 + DPTC))/ (273.16 + DPTC)
C      PR =      0.47*SR
C
C            THIS PROGRAM ILLUSTRATES THE SIMULATION RESULTS OF VARYING WPOTS
C
 14        DO 55 I = 1, 20
 15        CALL BALANS
```

```
16          CALL OUTPUT
17          WPOTS = WPOTS -0.5
18       55 CONTINUE
19          WRITE(6, 10)
20       10 FORMAT (1H1)
21          STOP
22          END

23          SUBROUTINE OUTPUT
24          IMPLICIT REAL ( A - Z )
25          INTEGER*4 I
      C
      C        PURPOSE OF THIS SUBROUTINE IS TO PRINT THE I/O RESULTS
      C
26          COMMON / PARAM1 / CL, EB, ERFC, HL, LE, LH, LR, NP, PB, RA,
           1                  RL, RLL, RLS, RLU, RTOT, RTOTC, SE,
           2                  SH, SR, TL, TLC, WPOT, WPOTS, WPTMIN
27          COMMON / PARAM2 / COMP, DRESP, FCNT, K1, K2, K3, LL, NPMAX,
           1                  RLMAX, RLMIN, SENS, SRPL, TLMINC
28          COMMON / PARAM3 / CA, ER, HA, HAIR, PR, SA, TA, TAC, TR, I
29          IF ( (I/2) * 2 .NE. I ) WRITE (6, 10)
30       10 FORMAT ( 1H1, ///)
31          WRITE (6, 20) CA, HA, PR, SA, TAC, TR, WPOTS,
           1              EB, HL, LE, CL, LR, NP, SE, RL, TR,
           2              RLS, TLC, WPOT, I
32       20 FORMAT ('0',' ENVIRONMENTAL INPUT PARAMETERS      ',/,
          AT5,'CA   =',F8.2,' G/M**3    ',T40,'HA   =',F8.2,' G/M**3    ',//,
          BT5,'PR   =',F8.2,' W/M**2    ',T40,'SA   =',F8.2,' M/S       ',//,
          CT5,'TAC  =',F8.2,' DEGC      ',T40,'TR   =',F8.2,' W/M**2    ',//,
          DT5,'WPOTS=',F8.2,' BAR       '                                 ,//,
          E ' SIMULATION OUTPUT    ',/,
          FT5,'EB   =',F8.2,' W/M**2    ',T40,'HL   =',F8.2,' G/M**3    ',//,
          GT5,'LE   =',F8.2,' W/M**2    ',T40,'CL   =',F8.2,' G/M**3    ',//,
          HT5,'LR   =',F8.2,' W/M**2    ',T40,'NP   =',F8.2,' G/(M**2*H)',//,
          IT5,'SE   =',F8.2,' W/M**2    ',T40,'RL   =',F8.2,' S/M       ',//,
          JT5,'TR   =',F8.2,' W/M**2    ',T40,'RLS  =',F8.2,' S/M       ',//,
          KT5,'TLC  =',F8.2,' DEGC      ',T40,'WPOT =',F8.2,' BAR       ',  /,
          L ' END OF SIMULATION SET', I4, ///)
33          RETURN
34          END

35          SUBROUTINE BALANS
36          IMPLICIT REAL ( A - Z )
37          INTEGER*4 COUNT, IEXIT, IFIN, INDEX, LOOP1, LOOP2
      C
      C        THE PURPOSE OF THIS SUBROUTINE IS TO SOLVE THE LEAF
      C        MODEL EQUATIONS USING NEWTON-RAPHSON ITERATIVE TECHNIQUE
      C
38          COMMON / PARAM1 / CL, EB, ERFC, HL, LE, LH, LR, NP, PB, RA,
           1                  RL, RLL, RLS, RLU, RTOT, RTOTC, SE,
           2                  SH, SR, TL, TLC, WPOT, WPOTS, WPTMIN
39          COMMON / PARAM2 / COMP, DRESP, FCNT, K1, K2, K3, LL, NPMAX,
           1                  RLMAX, RLMIN, SENS, SRPL, TLMINC
40          COMMON / PARAM3 / CA, ER, HA, HAIR, PR, SA, TA, TAC, TR, I
41          COMMON / CONSTA / A, B, C1, C2, C3, C4, DE, K, T1, T2, T3
42          DATA T1S, T2S, T3S / 1.0, 1.0, 1.0 /
43          ZERO = 1.0E-50
      C
      C        CONSTANT ZERO IS USED TO AVOID THE POSSIBILITY OF
      C        DIVISION BY 0.0
```

```
      C
   44         RA = 252.0 / (SQRT(SA/LL) + ZERO)
   45         SH = 1154.4 * 303.16 / TA
   46         HAIR = C3 * EXP ( C4 * (TA - 273.16) / (TA - 35.86)) / TA
      C
      C          AUXILIARY VARIABLES, DEFINED BY A1, A2, A3, ETC., ARE USED
      C          FOR THE SAKE OF CONVENIENCE IN WRITING LONG OR REPETITIVE EXPRES
      C
      C          IN GENERAL, VARIABLES OF THE DYX TYPE DENOTE THE DERIVATIVE
      C          OF Y WITH RESPECT TO X. FOR EXAMPLE, DEBTL AND DRTCCL MEAN
      C          THE DERIVATIVE OF EB WITH RESPECT TO TL AND THAT OF
      C          RTOTC WITH RESPECT TO CL, RESPECTIVELY.
      C
   47         A1 = EXP ( -K1 * COMP )
   48         A2 = EXP ( -K2 * PR )
   49         A3 = SRPL / LH
   50         IF(T1 .EQ. T1S .AND. T2 .EQ. T2S .AND. T3 .EQ. T3S) GO TO 1
   51         T1S = T1
   52         T2S = T2
   53         T3S = T3
   54         CONS = 2.0 / SQRT(3.14159)
   55         CALL TEMPFN
   56       1 CONTINUE
   57         HAP = HA
   58         IF ( HA .GE. HAIR ) HA = HAIR
      C
      C          GUESS INITIAL VALUES OF CL, TL AND RLS
      C
   59         CL = CA / 10.0
   60         TL = TA
   61         ERFC = ERF ((TL - 273.16) / TLMINC ) + ZERO
   62         RLS = RLMIN * (1.0 + K3 * CL) * EXP (-SENS * WPOTS) / ERFC
      C
   63         IF ( TL .GE. T2 ) TL = T2 - 1.0
   64         IF ( TL .LE. T1 ) TL = T1 + 1.0
   65         COUNT = 0
      C
      C          BEGIN NEWTON-RAPHSON CONVERGENCE LOOP
      C
   66         DO 2 LOOP1 = 1, 20
   67         A4 = ALOG ( TL / T1 ) + ZERO
   68         A5 = SQRT(TL)
   69         A6 = B * EXP ( -DE / (K * TL ))
   70         FCNT = A * A4 * A5 *    ( 1.0 - A6 )
   71         DFCNTL = (0.5 + 1.0/A4) * FCNT / TL - A*A4*A5*A6* DE / (K*TL**2)
   72         ERFC = ERF ((TL - 273.16) / TLMINC ) + ZERO
   73         A7 = C4 * (TL - 273.16) / (TL - 35.86)
   74         HL = C3 * EXP (A7) / TL
   75         DHLTL = HL * ( C4 * 237.3 / (TL - 35.86) ** 2 - 1.0/TL)
   76         A8 = RLMIN * (1.0 + K3 * CL) * EXP (-SENS * WPOTS) / ERFC
   77         DA8TL = -A8*CONS*EXP(-((TL-273.16)/TLMINC)**2)/(TLMINC*ERFC+ZERO)
   78         DA8CL = K3 * A8 / (1.0 + K3 * CL)
   79         IEXIT = -1
   80         RLMI = RLMIN
   81         RLMA = RLMAX
      C
      C          BEGIN THE SECOND CONVERGENCE LOOP .. LOOP WITHIN A LOOP
      C
   82         DO 3 LOOP2 = 1, 20
   83         COUNT = COUNT + 1
```

```
      RL = 1.0 / (1.0/RLS + 1.0/RLMAX)
      RLU = RL
      RLL = RL
      RTOT = 1.0 / (1.0/(RLU + RA) + 1.0/(RLL + RA))
      DRTOT = 0.5
      RLI = RL
      LE = LH * ( HA - HL) / RTOT
      DLERL = - LE * DRTOT / RTOT
C
C        WATER BALANCE EQUATION, (WPOT)
C
      WPOT = A3 * LE + WPOTS + WPTMIN
      DWPTRL = A3 * DLERL
      IF ( ABS(-SENS * WPOT) .GE. 174.0) GO TO 10
      RLS = RLMIN * (1.0 + K3 * CL) * EXP(-SENS * WPOT) / ERFC
      DRLSRL = - RLS * SENS * DWPTRL
      DRLRLS = (RLMAX / (RLMAX + RLS) ) ** 2
      A9 = 1.0/RLS + 1.0/RLMAX
      RLERR = RL - 1.0/A9
      DRLERR = 1.0 - DRLSRL * DRLRLS
      DELX = RLERR / DRLERR
      RL = RL - DELX
      IF(RL .LT. 0.0) RL = RLI / 2.0
      IF( DELX .LE. 0.0) RLMI = RLI
      IF( DELX .GE. 0.0) RLMA = RLI
      IF( RL .LE. ZERO) RL = ZERO
      IF ( ABS((RL - RLI) / RL ) .LT. IEXIT*1.0E-4) GO TO 5
      IF ( ABS((RL - RLI) / RL ) .LE.       1.0E-4) IEXIT = 1
    3 CONTINUE
C
C        END OF THE INTERIOR LOOP2
C
    5 CONTINUE
      SE = 2.0 * SH * (TA - TL) / RA
      LR = -2.0 * C1 * TL ** 4
      LE = LH * (HA - HL) / RTOT
C
C        ENERGY BALANCE EQUATION, (EB)
C
      EB = LE + LR + SE + TR
C
      DSETL = -2.0 * SH / RA
      DLRTL = 4.0 * LR / TL
      A10 = EXP ( - SENS * (WPOT - WPOTS) )
C
C        USING WPOT = - A3 * (LR + SE + TR) + WPOTS, THE DERIVATIVE OF RL
C        WITH RESPECT TO TL AND CL, DRLSTL AND DRLSCL RESPECTIVELY,
C        CAN BE OBTAINED AS FOLLOWS ..........
C
      DRLSTL = A3 * SENS * RLS * (DLRTL + DSETL) + A10 * DA8TL
      DRLSCL = A10 * DA8CL
      DRTOTL = DRTOT * DRLRLS * DRLSTL
      DRTOCL = DRTOT * DRLRLS * DRLSCL
      DLETL = - LH * ((HA - HL) * DRTOTL + RTOT * DHLTL) / RTOT ** 2
      DEBTL = DLETL + DLRTL + DSETL
      DEBCL = -LH * ( HA - HL) * DRTOCL / RTOT ** 2
C
      RTOTC = 1.0 / (1.0/(1.53 * RLU + RA) + 1.0/(1.53 * RLL + RA))
      DRTCTL = 1.53 * DRTOTL
      DRTCCL = 1.53 * DRTOCL
```

```
128         A11 = EXP ( - K1 * CL )
129         NP1 = (NPMAX * (A1 - A11) * (1.0 - A2) - DRESP ) * FCNT
130         NP = C2 * (CA - CL) / RTOTC
      C
      C           PHOTOSYNTHESIS BALANCE EQUATION, (PB)
      C
131         PB = NP1 - NP
132         DNP1TL = NP1 * DFCNTL / FCNT
133         DNP1CL = (NPMAX * (1.0 - A2) * K1 * A11 ) * FCNT
134         DNPTL = - NP * DRTCTL / RTOTC
135         DNPCL = - C2 * ((CA - CL) * DRTCCL + RTOTC ) / RTOTC ** 2
136         DPBTL = DNP1TL - DNPTL
137         DPBCL = DNP1CL - DNPCL
138         DELCL = (EB*DPBTL-PB*DEBTL) / ((DPBCL*DEBTL-DPBTL*DEBCL)+ZERO)
139         DELTL = - (EB + DEBCL * DELCL ) / (DEBTL + ZERO)
140         IFIN = 1
141         X = LOOP1
142         IF( TL .GT. T2) TL = (6.0*X*T2 + 2.0*T1) / (2.0 + 6.0*X)
143         IF( TL .LT. T1) TL = (7.0*X*T1 + 3.0*T2) / (3.0 + 7.0*X)
144         IF (( ABS(DELTL) .GE. 0.0001 * TL) .OR.
           1     ( ABS(DELCL) .GE. 0.0001 * CL)) IFIN = -1
145         TLC = TL - 273.16
146         IF ( IFIN .EQ. 1 ) GO TO 30
147         TL = TL + DELTL
148         CL = CL + DELCL
149         RLS = RLS + DRLSTL * DELTL + DRLSCL * DELCL
150         IF ( CL .LT. ZERO) CL = (CL - DELCL) / 2.0
151       2 CONTINUE
      C
      C           END THE CONVERGENCE LOOP
      C
152      10 WRITE (6, 20) LOOP1, COUNT
153      20 FORMAT ('0','     BALANS DID NOT CONVERGE IN',I4,' ITERS. OF LOOP1
           1AND',I4,' ITERS. OF LOOP2')
154      30 CONTINUE
155         RETURN
156         END

157         SUBROUTINE TEMPFN
158         IMPLICIT REAL (J - N )
      C
      C           PURPOSE OF THIS SUBROUTINE IS TO DETERMINE THE VALUES OF THE
      C           CONSTANTS A, B, AND DE OF THE TEMPERATURE RESPONSE FUNCTION FCNT
      C           ( SEE SUBROUTINE BALANS )
      C
159         COMMON / CONSTA / A, B, C1, C2, C3, C4, DE, K, T1, T2, T3
160         ZERO = 1.0E-50
161         ALPHA = ( 1.0 / T3 - 1.0 / T2 ) / K
162         BETA = K * T3 ** 2
163         GAMMA = ( 1.0 / ALOG ( T3 / T1 ) + 0.5 ) / T3
164         DEMIN = ( 1.0 - ALPHA * BETA * GAMMA ) / ALPHA
165         DEMAX = 140.0 / ALPHA
166         DE = 1.001 * DEMIN
167         GB = BETA * GAMMA
168         DO 1 I = 1, 40
169         EX = EXP (-ALPHA * DE)
170         F = EX * (DE + GB) - GB
171         DF = EX - (DE + GB) * ALPHA * EX
172         DES = DE
173         DELTA = - F / (DF + ZERO)
```

```
174         IF(ABS(DELTA) .GT. 2.1*ABS(DES)) DELTA = DELTA/ABS(DELTA)*DES
175         DE = DE + DELTA
176         IF ( DE .GE. DES ) DEMIN = DES
177         IF ( DE .LE. DES ) DEMAX = DES
178         IF ( DE .LT. DEMIN ) DE = (6.0*DEMIN + DEMAX) / 7.0
179         IF ( DE .GT. DEMAX ) DE = (7.0*DEMAX + DEMIN) / 8.0
180         IF ((DEMAX - DEMIN) .LT. (1.0E-6 * DES)) GO TO 2
181       1 CONTINUE
182         WRITE(6, 10) T1, T2, T3, ALPHA, BETA, GAMMA,
           1             DEMAX, DEMIN, DE, DES, GB
183      10 FORMAT ('0', '   CONVERGENCE IN ENERGY IN ERROR', / ,
           1           6E16.7, / , 6E16.7 )
184         GO TO 30
185       2 DE = DES
186         B = EXP ( DE / (K * T2))
187         A=1./(SQRT(T3)*ALOG(T3/T1)*(1.-EXP(-DE/ K*(1./T3-1./T2))))
188         T1C = T1 - 273.16
189         T2C = T2 - 273.16
190         T3C = T3 - 273.16
      C
      C         IF EXECUTION OF THE FOLLOWING WRITE STATEMENT IS NOT DESIRED
      C         PLACE A RETURN CARD IMMEDIATELY PRECEDING IT.
      C
191         WRITE ( 6, 20 ) A, B, DE, T1C, T2C, T3C
192      20 FORMAT ('0','A =',E14.6,', B =',E14.6,', DE =',E14.6,
           1          ', T1C =',F7.2,', T2C =', F7.2,', T3C =',F7.2,//)
193      30 RETURN
194         END

195         BLOCK DATA
      C
      C         THE PURPOSE OF THIS SUBPROGRAM IS TO SUPPLY FIXED PARAMETERS
      C         AND CONSTANTS OF THE MODEL.
      C
196         COMMON / PARAM1 / CL, EB, ERFC, HL, LE, LH, LR, NP, PB, RA,
           1                  RL, RLL, RLS, RLU, RTOT, RTOTC, SE,
           2                  SH, SR, TL, TLC, WPOT, WPOTS, WPTMIN
197         COMMON / PARAM2 / COMP, DRESP, FCNT, K1, K2, K3, LL, NPMAX,
           1                  RLMAX, RLMIN, SENS, SRPL, TLMINC
198         COMMON / PARAM3 / CA, ER, HA, HAIR, PR, SA, TA, TAC, TR, I
199         COMMON / CONSTA / A, B, C1, C2, C3, C4, DE, K, T1, T2, T3
200         REAL K, K1, K2, K3, LH, LL, NPMAX
201         DATA C1      , C2     , C3     , C4      /
           1      5.67E-8, 3600.0, 1323.5, 17.2694/
202         DATA K / 8.617065E-5 /
203         DATA K1 , K2   , K3   /
           1      5.0, 0.01, 10.0/
204         DATA T1     , T2     , T3     /
           1      278.16, 318.16, 308.16/
205         DATA LH     , LL   , RLMAX   , RLMIN, SRPL/
           1      2442.0, 0.05, 10000.0, 40.0 , 50.0/
206         DATA COMP, DRESP, NPMAX, SENS, TLMINC, WPTMIN/
           1      0.02, 0.5  , 20.0 , 0.3 , 30.0  , -5.0  /
      C
      C         DEFINITION OF FIXED PARAMETERS AND CONSTANTS ---------
      C
      C         C1, C2, C3, C4 = CONSTANTS AS USED IN MODEL EQUATIONS
      C                          ( SEE SUBROUTINE BALANS)
      C         COMP = CO2 COMPENSATION POINT (G/M**3)
      C         DRESP = DARK RESPIRATION RATE (G/HR*M**2)
```

```
C          K = BOLTZMANN CONSTANT (EV/K)
C          K1, K2, K3 = CONSTANTS AS USED IN MODEL EQUATIONS OF NP1 AND RLS
C          LH = LATENT HEAT OF VAPORIZATION OF WATER (J/G)
C          LL = LEAF DIMENSION (M)
C          NPMAX = MAXIMUM GROSS PHOTOSYNTHESIS (G/M**2*HR)
C          RLMAX = MAXIMUM LEAF RESISTANCE (S/M)
C          RLMIN = MINIMUM LEAF RESISTANCE (S/M)
C          SENS = STOMATAL SENSITIVITY TO WATER POTENTIAL (1/BAR)
C          SRPL = SPECIFIC RESISTANCE OF PLANT (BAR*S/M**2/G)
C          T1, T2 = LOWER AND UPPER LIMITS OF TEMPERATURE (ABSOLUTE SCALE),
C                   RESPECTIVELY, AT WHICH PHOTOSYNTHESIS OCCURS
C          T3 = TEMPERATURE (ABSOLUTE SCALE) AT WHICH MAXIMUM PHOTOSYNTHESI
C               OCCURS
C          TLMINC = REFERENCE TEMPERATURE (CENTIGRADE SCALE)
C                   FOR STOMATAL OPENING
C          WPTMIN = MINIMUM LEAF WATER POTENTIAL (BAR)
C
  207          END

       //$DATA

A =  0.648001E 00, B =  0.141952E 27, DE =  0.165093E 01, T1C =    5.00, T2C =  45.
```

```
 ENVIRONMENTAL INPUT PARAMETERS
  CA    =     0.57 G/M**3          HA    =    18.10 G/M**3

  PR    =   300.00 W/M**2          SA    =     2.00 M/S

  TAC   =    30.00 DEGC            TR    = 1090.00 W/M**2

  WPOTS=     0.00 BAR

 SIMULATION OUTPUT
  EB    =     0.03 W/M**2          HL    =    31.19 G/M**3

  LE    =   -95.33 W/M**2          CL    =     0.08 G/M**3

  LR    =  -964.46 W/M**2          NP    =     3.56 G/(M**2*H)

  SE    =   -30.19 W/M**2          RL    =   630.83 S/M

  TR    =  1090.00 W/M**2          RLS   =   673.32 S/M

  TLC   =    30.52 DEGC            WPOT  =    -6.95 BAR
 END OF SIMULATION SET    1


 ENVIRONMENTAL INPUT PARAMETERS
  CA    =     0.57 G/M**3          HA    =    18.10 G/M**3

  PR    =   300.00 W/M**2          SA    =     2.00 M/S

  TAC   =    30.00 DEGC            TR    = 1090.00 W/M**2

  WPOTS=    -0.50 BAR

 SIMULATION OUTPUT
  EB    =     0.03 W/M**2          HL    =    31.34 G/M**3

  LE    =   -89.22 W/M**2          CL    =     0.07 G/M**3

  LR    =  -965.55 W/M**2          NP    =     3.32 G/(M**2*H)

  SE    =   -35.20 W/M**2          RL    =   684.70 S/M

  TR    =  1090.00 W/M**2          RLS   =   735.04 S/M

  TLC   =    30.61 DEGC            WPOT  =    -7.33 BAR
 END OF SIMULATION SET    2


 NO FURTHER SETS ARE SHOWN
```